NORTH PACIFIC ANADROMOUS FISH COMMISSION

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Status of Pacific Salmon and Their Role in North Pacific Marine Ecosystems

Edited by: Richard Beamish and Vladimir Radchenko

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North Pacific Anadromous Fish Commission

The elegant woodblock print on the cover is the work of Tomoko Watanabe, a Japanese artist who lives in Vancouver, BC, Canada.

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Getting the Message Out

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Abstract: Total Pacific salmon production as indicated by the total catch of all Pacific salmon-producing countries is at historic high levels. Most scientists agree that the current high levels of production result from favourable ocean and climate conditions. There also is agreement that the technology and international cooperation exist to establish an international program that will determine the processes that regulate Pacific salmon abundance and develop reliable forecasting models. Combining information on production of salmon from fresh water or hatcheries with an understanding of how ocean conditions regulate marine survival will identify for the first time the processes regulating recruitment. This understanding will provide regional fisheries managers with new models that more accurately link climate and physical processes to recruitment, abundance and distribution. An international team of researchers can carry out the required research within the organization established for the North Pacific Anadromous Fish Commission if private and public funds are available. In order to receive these funds, researchers need to convince funding agencies that they are committed, capable and accountable. Open, honest and direct communication with clients and patrons will establish the trust needed to carry out the long-term research that will provide managers with the models needed to manage Pacific salmon in a future dominated by the impacts of climate change.

Keywords: integrated ocean studies, communication of Pacific salmon research, North Pacific Anadromous Fish Commission

WHAT IS THE MESSAGE?

The first message is that Pacific salmon are at high levels of abundance. In fact, the catches by all countries were at historic high levels in 1995 and the second largest catch occurred in 2003 (Fig. 1A). Catches of all Pacific salmon in Alaska followed a similar pattern with historic high catches in 1995, 1999 and 2005 (Fig. 1B). This is important information for the large numbers of people around the rim of the North Pacific that care about Pacific salmon.

The second message is that climate profoundly affects the production of Pacific salmon. It is self-evident that the weather would affect the survival of Pacific salmon. However, it was only recently that it became known that the kind of climate variability that affects Pacific salmon occurs as trends rather than varying randomly. The recognition of the occurrence of trends in climate is important because the capacity of the ocean to produce salmon also changes in trends as evidenced by the large-scale synchrony in catch trends around the subarctic Pacific. The challenge of this discovery for salmon stewardship is two-fold. Firstly, there will be shifts from periods of high ocean survival to low ocean survival that will occur quickly. These shifts need to be predicted or at least quickly recognized when they occur to allow management to reduce catches and adjust enhancement programs. Secondly, the accumulation of greenhouse gases

is expected to change climate in ways that will affect salmon. At this time, we do not understand what these changes will be.

The third message is that technology and international partnerships exist that can identify the processes that regulate Pacific salmon production. The picture of stock structure and migration timing that we see today resulted from the life-history strategy that the various species of Pacific salmon evolved to maximize their production in the naturally changing ocean and in fresh water. We now need to put together the pieces of the puzzling process (Ricker 1972, 1973) that regulates the abundance of Pacific salmon.

WHY THE MESSAGE NEEDS TO GET OUT

There is a general impression among the public and even some salmon biologists that Pacific salmon are following the same fate as some well-publicized species in the North Atlantic and other areas. It is true that some stocks of some species no longer exist and some stocks are in critically low abundance. However, these examples must be seen in the perspective of all Pacific salmon. When this is done, it becomes clear that the importance of Pacific salmon extends beyond individual stocks. Pacific salmon are the dominant group of fishes in the daytime in the surface waters of the subarctic Pacific (Beamish et al. 2005). Extensive surveys by Japanese, Russian, United
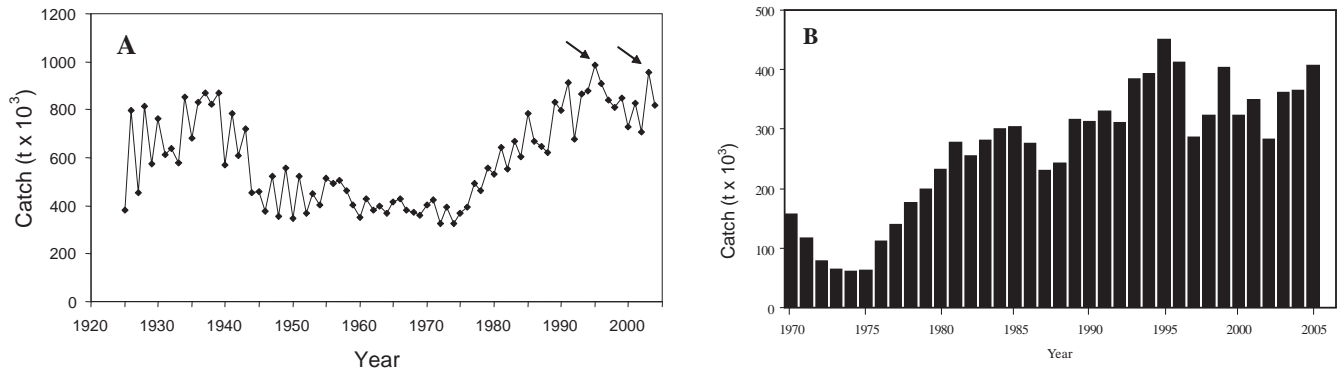
Fig. 1. (A) Total catch of Pacific salmon by all countries from 1925 to 2004. The largest catches occurred in 1995 and 2003 (arrows). From 1990 to 2004, catches of pink, chum and sockeye salmon represent an average of 95.7% of the annual total catch. Coho and chinook salmon represent an average of 4.7%. (B) Catch in Alaskan waters from 1970 to 2005. (data from the North Pacific Anadromous Fish Commission statistical yearbook, 2002, and historical data, http://www.npafc.org.)

States and Canadian scientists have documented the species composition of fishes living in the top 40 m of the waters north of the chlorophyll boundary (Fig. 2) which indicates the vastness of the potential feeding area. These studies show that, in general, pink (*Oncorhynchus gorbuscha*), chum (*O. keta*) and sockeye (*O. nerka*) salmon are the dominant group of fishes in the vast feeding area extending through the Bering Sea. The high catches of salmon over the past decade indicate that the climate and ocean processes in this feeding area have increased the capacity of the ocean to produce Pacific salmon. It is important that people know that these changes occurred so that they will understand the importance of identifying these processes that affect the capacity of this ocean area to produce salmon. Furthermore, it is of general interest to know the role that salmon play in these large marine ecosystems. The management philosophy in many countries is changing from a focus on single species to an ecosystem approach. This makes sense and is a long overdue approach to Pacific salmon stewardship. The difficulty is the cost of the required research. Thus, it makes sense to combine research efforts to make the best use of available funds. It is time for an international study of the processes that connect climate to salmon production in fresh water and in the ocean and to sort out the ecological relationships among salmon and with other species. The Bering-Aleutian Salmon International Survey (BASIS) program (North Pacific Anadromous Fish Commission 2001) and the resulting cooperation that developed among "salmon" scientists within the North Pacific Anadromous Fish Commission (NPAFC) is a foundation that will support fully integrated international studies that will resolve the long-standing mysteries of Pacific salmon production.

THE NEED FOR OPEN, HONEST AND CREDIBLE ADVICE

Feynman (1998) wrote that honesty in science was telling intelligent people what they needed to know to make intelligent decisions. Scientists traditionally debate interpretations

in the peer-reviewed literature. Environmentalists take their messages to the public and politicians using the popular media. In the past, the two approaches proceeded along their own paths as funding for the work of scientists was usually adequate to support studies on the scale of enquiry at a single-species level. Scientists tended to talk within their own community, leaving the public communication of science to the environmental community. The recognition of the critical role of climate in the regulation of salmon abundances and the increasing levels of greenhouse gases essentially changes everything. Both groups now need to communicate more effectively among themselves and among the public.

The scientific community needs to carry out expensive, long-term research in the ocean that is linked to freshwater or hatchery production. Government agencies in Pacific salmon-producing countries can provide ships for internationally coordinated programs but all of the money for research is not available through the traditional government agencies.
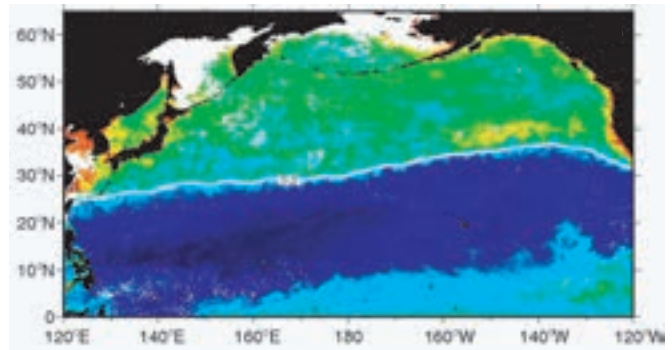
Fig. 2. Satellite imagery of surface chlorophyll *a* (from King 2005) showing the sharp boundary between the relatively high levels in the north (green) and the lower levels in the warmer sub-tropical regions (blue). The boundary between the two regions is the Transition Zone Chlorophyll Front. This boundary moves north in the summer and south in the winter. The average distributions of Pacific salmon (Beamish et al. 2005) are between 40° and 50°N in the high chlorophyll *a* area.
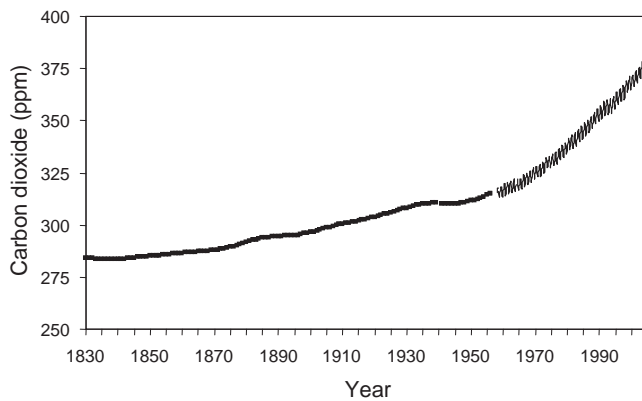
Fig. 3. Increase in atmospheric carbon dioxide levels from 1832 to 2004. Data from 1832 to 1958 are historical CO_2 data measured from Law Dome, East Antarctica ice cores and has been smoothed using 20-year running averages (Source: Etheridge et al. 1998). Monthly data from 1958 to 2004 are from Mauna Loa (Source: Keeling 2004).

Adequate funding would be available if philanthropic organizations were to enter into cooperative arrangements with government agencies. In the past these funding organizations favoured people who appeared independent of government. The reality is that for Pacific salmon stewardship, the future for both groups is all about climate and climate change. In the environmental movement there is debate about their future roles. One view is that the current approach to environmentalism must die so that a bold new direction is possible (Shellenberger and Nordhaus 2005). Proponents of the need to start over argue that the environmental movement is fragmented and generally unsuccessfully addressing the serious problem of global warming. There is no question that this is true for Pacific salmon. It is very hard to find scientific programs that are currently researching the impacts of global warming on Pacific salmon production. The problem of understanding climate change impacts on the dynamics of salmon in the ocean rearing area is not going to be solved by providing money to either groups that do not create new knowledge or individuals working on projects that are not part of integrated studies. It is time to do things differently. It is time for a trusted group of experts to speak openly, plainly and honestly to the public about what is known and what needs to be known about the factors affecting salmon abundance. The general public and funding organizations need to be directly involved with the researchers who are on the front line. The research that is needed to address the issues of global warming impacts will require the funding support of philanthropic organizations, and to get this, government researchers need to acquire the trust and support of the general public. People need to hear about Pacific salmon directly from the source. There is no dispute that CO_2 is increasing in the atmosphere (Fig. 3) and it is most likely that the increases will continue as the economies of countries such as China increase their energy demands. It has been reported (Elliot et al. 2002) that China expects to quadruple its economy in 30 years using new ener-

gy from burning coal that is equal to 50% of the current energy used in the U.S.A. Clearly, climate will be the major issue for Pacific salmon over the careers of at least several generations of biologists. Within NPAFC there is the understanding to know that change is needed. There is the technology to do the needed research. There are ships. There is an organization that is responsible, recognized and accountable. It is now time to expand the thinking and establish international research teams within the NPAFC.

WHAT SCIENCE NEEDS TO BE DONE?

My list of what needs to be done should be viewed as ingredients for discussion. The list does not include activities associated with the freshwater phase of Pacific salmon, but the anadromous life history of salmon requires an understanding of the factors affecting their dynamics in both fresh water and the ocean. It is important and preferable that any marine program is closely linked to the freshwater stages of the particular species and stocks; however, the following is a focus for marine research.

1. Regime shifts change trends in the productivity of Pacific salmon, but what causes the shift in regimes? Recently, a task team of international scientists confirmed that regimes are real (King 2005). Their investigations confirmed the observations of others that regime shifts occurred in 1989 and 1998 as well as the now well-known 1977 regime shift. After the 1998 regime shift, biological productivity improved in the southern regions of the eastern North Pacific and in the northern regions of the western North Pacific. The existence of shifts in trends in biological production and the observation of synchronous trends in salmon catch are evidence that there is a carrying capacity for Pacific salmon. A recognition of a carrying capacity for salmon means that it is necessary to be able to determine when these shifts in productivity occur. One way to determine when regime shifts occur is to discover the physical mechanism that causes regimes to shift. Beamish et al. (1999, 2007) proposed that this mechanism is associated with solar cycles and thus has a connection to the physics of planetary energy distribution. If this is true, it may be possible to identify regime shifts by studying the causes rather than the impacts.

2. What are the key biological, climatic and oceanographic factors affecting long-term changes in Pacific salmon production and distribution? In 1973, W.E. Ricker noted that a puzzling problem of Pacific salmon ecology was that runs of salmon to major rivers could not be managed so that their abundances could be increased to levels that generally were expected based on their past history. We now know that the capacity of the ocean to produce salmon improved after the 1977 regime shift. The explanation to the puzzling problem was that climate and ocean conditions affected the capacity of the ocean to produce salmon non-randomly. It is now timely to determine what

these conditions are.

3. What are the similarities in production trends among salmon populations around the subarctic Pacific? This is a problem of indexing. Is it possible to identify small groups of salmon that are indices of the production trends of larger groups? It will never be possible to study the responses of all stocks, so it is important to find key aggregates of stocks that are indicators of production trends.

4. What are the seasonal migration patterns of salmon from each salmon-producing country? There is a common pasture in the ocean, but how much of this common pasture is used by how many stocks of what particular countries? This is particularly relevant to the question of how the enhanced production of one country might affect the production of another country.

5. How is the carrying capacity for salmon affected by trends in climate? There is a relationship between large-scale patterns in atmospheric circulation and Pacific salmon production (Beamish et al. 1999). What is not known is how changes in atmospheric circulation will affect biological productivity. How will global warming change atmospheric circulation, ocean currents and upwelling? For example, how will the chlorophyll boundary (Fig. 2) change? There are global climate change models of ocean temperature changes, but the large-scale changes in atmospheric circulation over the subarctic Pacific resulting from global warming need to be determined so that changes in ocean currents can be modeled.

6. What is the relationship between the dynamics of region-al stocks and the dynamics of the species throughout its range? Each species of Pacific salmon has evolved to maximize its abundance by competing with other species of salmon for food and habitat. The success of a species may relate to the ability of some regional stocks to survive better than other regional stocks during specific climate and ocean conditions. This could mean that populations in one country will contribute to production in another country. This could be particularly important if future climate changes increase the ocean carrying capacity for salmon (Beamish and Noakes 2002). Research would also attempt to solve long-standing questions relating to cyclic dominance and stock biodiversity.

7. How will the distributions and abundances of species be affected by global warming? Will species at the southern limits of their distribution be affected first and will the impacts be greater in fresh water or in the ocean? Will some species establish new runs farther north and into the Arctic? Will hatchery-reared fish survive equally as well as wild fish?

8. How do we forecast trends in abundance and changes in migration timing? Recent controversies over sockeye salmon returning to the Fraser River (Fig. 4) indicate that there is an urgent need to improve our ability to forecast. Even when abundances are exceptional (Fig. 5), it is apparent that better forecasts will result in better use of fish surplus to spawning requirements.

9. How do we communicate effectively with the general public? All science has patrons. We must accept that an
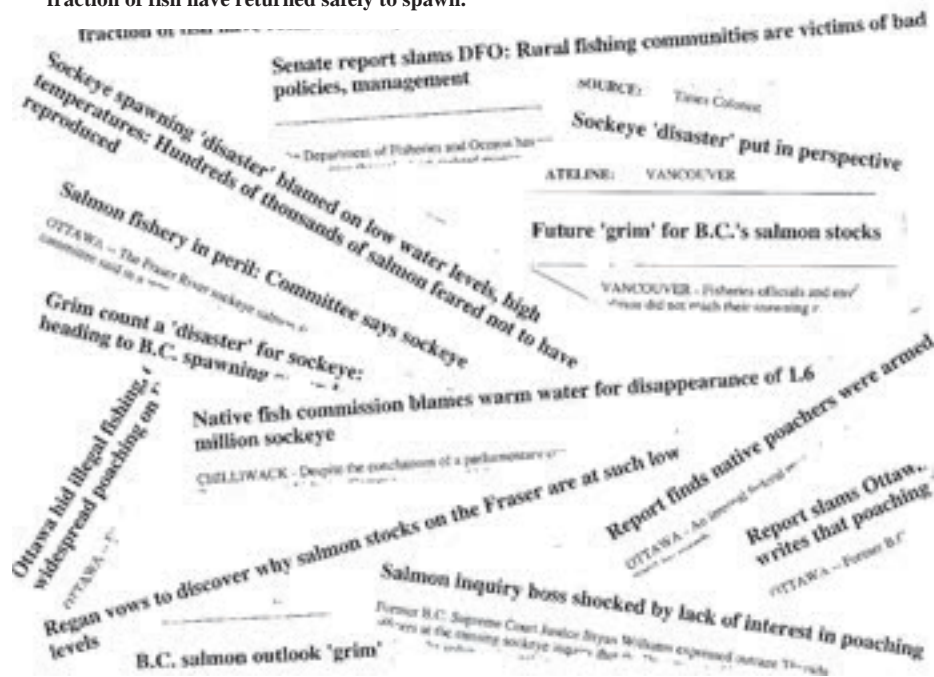
Fig. 4. Example of some of the newspaper clippings in British Columbia in 2004.

investment of public and private funds must be matched by strategic thinking and accountability in science and in the communication of science.

10. How are teams of researchers selected, recognized and rewarded? Scientists are recognized for individual achievement and not for teamwork. New rewards systems are needed.

HOW DO WE DO IT?

The North Pacific Anadromous Fish Commission established the Bering–Aleutian Salmon International Survey (BASIS) program in 2001 (North Pacific Anadromous Fish Commission 2001). The initial goal of the program was to determine how ocean conditions affected the survival and growth of Pacific salmon. The program resulted in unprecedented cooperation among salmon-producing countries and their researchers. Visiting scientists were welcomed on research vessels. Data and samples were freely exchanged. Each year, the preliminary results of the various cruises were provided to all interested researchers. Cooperation was so good that researchers at sea would accept email requests to

Fig. 5. Pink salmon carcasses on a beach in Alaska. Photo courtesy of Jim Lavrakas, Anchorage Daily News, Anchorage, AK 99508.

collect data. This timely and open communication effectively provided millions of dollars of research information to all participating countries. The opportunity to work together resulted in a cooperative spirit that is characteristic of any successful team. The NPAFC currently has a science committee and an enforcement committee. I propose that a third committee is needed to manage the expanded ocean and climate impacts program. The expanded program would follow the model of BASIS but would include all areas of the ocean and would encourage research that links information from fresh water and hatcheries with ocean research. This third committee would be managed by an International Board consisting of representatives from each country (Fig. 6). Eventually, Board members would have to represent the interests of funding agencies and the general community of people who are passionate about Pacific salmon. There would be a science panel reporting to the management board that would be responsible for the coordination and reporting of research. The actual research would be carried out by teams (Fig. 6).

The Management Board would represent national governments and manage communications. The Board would be responsible for funding and would maintain the central research focus. The Board would request that a science plan be developed by the Science Panel. The Science Panel would consist of about 10-12 scientists that would represent a variety of disciplines as well as the participating countries. The Science Panel would include scientists not affiliated with the NPAFC. The Panel would elect a chair and would have administrative support. The Panel would establish a strategic research plan that would be approved by the Board. The Panel would establish research teams and associated support programs such as the use of ships. The Panel would maintain databases, review and write proposals and evaluate the results of privately funded research. Panel members would also be the communicators of research results by working within a communication strategy established by the Board. Each science team would conduct the directed research. Teams would usually contain an integrated and diverse group of experts that would reflect the need to link biology, oceanography, climatology, mathematics and common sense. Teams would use models wisely. Teams would meet as needed to continually assess what is known and what needs to be known. Teams would publish their results. The end point of fisheries science should be the ability to forecast salmon production at a level that protects stocks and sustains fisheries. The Management Board would ensure that forecasting is emphasized. If foundations provide funding, it will be expected that the resulting data are eventually made available to others. Thus a consequence of an international research program would require open and easy access to data.

CONCLUSION

For decades we have studied small pieces of the puzzling life-history strategy of Pacific salmon. We now have the tech-
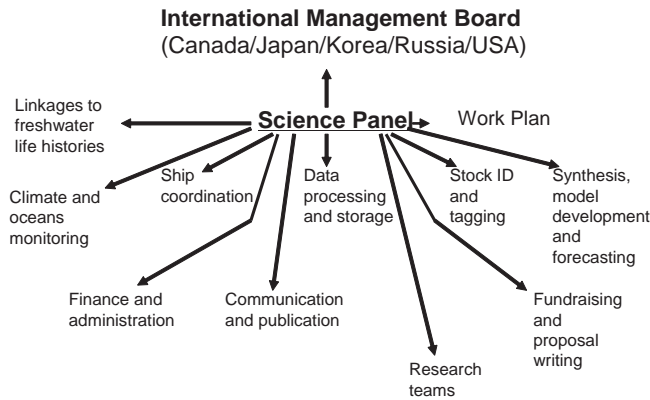
Fig. 6. Proposed organizations of a Committee within the NPAFC that would plan, coordinate and evaluate an international research program.

nology and cooperation needed to understand how recruitment of Pacific salmon is regulated. It is time to combine all of the resources available to finally put the pieces of the puzzle together. In order to secure the funding needed to support the international teams, it is necessary that the general public and funding agencies have a clear understanding of what is known and what needs to be known. Direct, open, honest and trustworthy relationships need to be established between front-line researchers, the general public and funding agencies. The NPAFC is perfectly positioned to coordinate a new international program, but environmental groups and funding agencies must be part of the coordinated effort. NPAFC will have to find ways to garner their support, perhaps through inclusion in the Management Board. Global climate change is the most serious threat to the future management of Pacific salmon stocks. The information needed to manage salmon through this period of climate change can now be obtained. It is a matter of money, leadership and teamwork.

ACKNOWLEDGEMENTS

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Preface

The International Symposium on the Status of Pacific Salmon and Their Role in North Pacific Marine Ecosystems was held at the Lotte Hotel on beautiful Jeju Island, Republic of Korea, between October 30 and November 1, 2005. The Symposium was hosted by the North Pacific Anadromous Fish Commission (NPAFC), and co-sponsored by the North Pacific Marine Science Organization (PICES). Dick Beamish and Vladimir Radchenko co-chaired the steering committee consist of: Jack Helle, Yukimasa Ishida, Vladimir Karpenko, Suam Kim, Kate Myers, Toru Nagasawa, Ian Perry, John Stein, and Vladimir Sviridov. All necessary arrangements were made by the NPAFC Secretariat in cooperation with the Organizing Committee and local coordinators. There were 32 oral, and 20 poster presentations followed by a wrap-up discussion session. This bulletin includes 31 papers which were peer reviewed and edited. Reviewers are listed at the end of the bulletin.

Trends in Abundance and Biological Characteristics of Pink Salmon (*Oncorhynchus gorbuscha*) in the North Pacific Ocean

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Abstract: Pink salmon are the most widely distributed species of the genus *Oncorhynchus*. Biennial cycles in the timing of the spawning migration and catch values are characteristic of pink salmon stock dynamics. Over the long term, two periods of high levels of abundance have been observed on both the Asian and North American coasts of the Pacific Ocean. Large-scale trends in abundance vary less than regional abundances. Coincidences in trends in catch dynamics among odd-year and even-year broodlines were found for several fishery regions. The observed relationships suggest a response of both broodlines to global factors that influence pink salmon reproduction and survival. Trends in abundance are influenced by global factors that are not necessarily cyclical. The dynamics of solar activity and an increase in ocean heat content play a significant role in their cumulative effect. Current pink salmon stock abundance may be close to a historic maximum. There is reason to expect that this level will continue in the near future under the influence of increasing ocean heat content. Pink salmon biological characteristics are related to levels of stock abundance. Average size in specific regions can also be related to the structure of regional salmon stocks which consist of a variety of seasonal races and ecological groupings.

Keywords: pink salmon, abundance dynamics, solar activity, ocean heat content

INTRODUCTION

Pink salmon (*Oncorhynchus gorbuscha*) are the most widely distributed Pacific salmon species of the genus *Oncorhynchus*. They occupy an area from 38° N in the Sea of Japan to the Aleutian Island and from the southeastern Sea of Okhotsk to the Gulf of Alaska where they overwinter (Heard 1991; Shuntov 1994). In contrast to other Pacific salmon, the distribution of pink salmon extends into the Arctic. At their southernmost distribution, spawning pink salmon populations enter rivers from Hokkaido and the northern Korean Peninsula to the Lena River in Asia, and from the Sacramento River in California to the Mackenzie River in Arctic Canada. Most spawning populations are situated between 45° and 65°N (Mathisen 1994; Temnykh 2005). The most abundant pink salmon populations spawn in rivers of Sakhalin and the southern Kuril Islands, the western and eastern coasts of the Kamchatka Peninsula, and central and southeastern Alaska.

Human introductions have created several pink salmon stocks beyond the Pacific Ocean. One of the largest acclimatized stocks is well established in the Great Lakes in the United States and Canada (Kocik et al. 1991). In 1956, pink salmon were accidentally introduced into Lake Superior in very small numbers (about 100 fish). Since that time, they have become permanent members of the pelagic ecosystem in Lake Superior, Lake Huron and Lake Michigan (Kelso and Noltie 1990). Despite significant changes in life span (some fish mature at 3 and even 4 years of age) two-year cycles in the abundance of pink salmon were observed in the St. Marys River that connects Lake Superior and Lake Huron. There, catch-per-unit-effort was greater in even years (57 fish/night) than in odd years (30 fish/night) (Kennedy et al. 2005) indicating the dominance of the even-year cycle.

In Russia, pink salmon have been introduced into the Barents and White seas. Pink salmon spawning migrations in these areas reached 155,400 fish in 2001. Fish from this stock have strayed to Iceland, Scotland and as far as the southern coast of Norway. However, it was only the odd-year broodline that reproduced successfully. All efforts to produce an even-year broodline have been unsuccessful despite the fact that the same technology was used for both lines. The odd-year and even-year broodlines have significantly different gene pools. The levels of divergence along their respective genetic markers are higher than between the different local groups within each of these broodlines (Glubokovsky 1995).

One of the most characteristic features of pink salmon abundance dynamics is their two-year life cycle. The levels of spawning stock abundance differ markedly between odd- and even-year broodlines: high levels in odd years and low

levels in even years, and *vice versa*. The dominance of even-year or odd-year populations, may persist for long periods of time while stocks in neighboring regions may show the opposite dynamics; for example, on the western and eastern Kamchatka coasts, respectively. Therefore, we analyzed the trends in abundance and biological characteristics of pink salmon, paying special attention to both similarities and differences between odd-year and even-year broodlines. Additional attention was paid to recently revealed coincidences in trends for some regional groups (Radchenko 2004). The causes and applicability of this phenomenon for forecasting pink salmon abundance dynamics are discussed.

Preliminary analysis reveals two important global climate factors that affect pink salmon stock abundance. The first is the influence of precipitation and air temperature on the spawning grounds, especially in winter and early spring (Goryainov & Shatilina 2003). The second is the influence of atmospheric circulation patterns on surface water along feeding and migration routes. On a global scale, variability in these climate parameters is determined by interrelated, but different, global processes with different periodicities. The patterns of atmospheric circulation are determined by the earth's rotation velocity (Klyashtorin and Sidorenkov 1996). Variability in air temperature is related to solar activity although it does not depend on the intensity of long-wave radiation directly. Below, we also analyze the long-term dynamics in the average annual values of the Wolf numbers, which characterize solar activity.

MATERIALS AND METHODS

Catch dynamics is the basic index of Pacific salmon stock abundance. This index remains as almost the only measure of abundance for large geographical regions, that is obtained by direct observation. Most other indices are determined using extrapolation to some degree. In this connection, we pay significant attention to the analysis of Pacific salmon catch statistics (Chigirinsky 1993; Henderson and Graham, 1998; Hiroi 1998; Kope and Wainwright 1998; Radchenko 1998; Karpenko and Rassadnikov 2004; Eggers et al. 2004).

Data analysis of the absolute abundance of pink salmon seems to be preferable to reveal trends and regularities in abundance dynamics. However, such data series are still rare and relatively short in the majority of regions. Observations of pink salmon absolute abundance have been actively conducted in the major fishery regions on the Russian coast since the beginning of the 1960s. Varnavskaya et al. (1995) compared dynamics of pink salmon catch and absolute abundance (i.e. catch + escapement) in 1960–1993. They noted that distinctions are negligible in most cases, although sometimes, such as for the odd-year broodline in western Kamchatka, the northern Okhotsk Sea coast, the Amur River and the Primorie region, discrepancies between catch data and spawner abundance are clearly recognizable. However, the portion of pink salmon catch in those regions averaged only

16.1% of the total pink salmon harvest on the Russian coast in odd years between 1960 and 1993. Catch and absolute abundance data summarized by Antonov (2005) for Aniva Bay have a close correlation ($R^2 = 0.97$) for 1971–2004. This indicates that it is appropriate to use pink salmon catch data for analysis of abundance dynamics, at least for the period after stabilization of fishery.

Data on the total pink salmon catches on the Asian and North American coasts for 1925–2001 were taken from the review prepared by the Working Group on Stock Assessment (CSRS) of the North Pacific Anadromous Fish Commission (Eggers et al. 2004). The catch series for the Russian coast for 1900–1986 are based on the statistical summary (Yanovskaya et al. 1989) prepared by the All-Russian Scientific Research Institute of Fisheries and Oceanography (VNIRO, Moscow). Data for 1900–1906 are incomplete and include information from the Sakhalin – Kuril Island region only. Data for 1940–1947 were taken from Tables 5 and 10 from Yanovskaya et al. (1989). Information on the Japanese catch on southern Sakhalin and Kuril Islands and areas of the concession fishery were taken from the INPFC Bulletin No. 39, Table 43, 1979. Total weight was estimated from catch in numbers multiplied by the average pink salmon body weight (1,300 g for 1936–1942) in several Sea of Okhotsk coastal fishery regions. Since Japanese data on this pink salmon fishery became available (Eggers et al. 2004), they were included in the total Japanese catch calculation of the present-day Russian coast for 1925–1945. A comparison of two data series revealed that the previous pink salmon harvest was underestimated in those years. The average catch from the CSRS report (109,110 t for the 21 years) exceeds the estimate (101,980 t) from the VNIRO report by 6.5%. Therefore, the catch data series for 1906–1924 from the VNIRO report were corrected by a multiplication factor of 1.07. Catch data for the Russian fishery on the eastern and western Kamchatka coasts were not available for 1931 and 1933. Only data from the Japanese concession fishery were used in the analysis for those years: 6,817 (1931) and 17,330 t (1933) (eastern coast); 10,250 and 10,350, respectively, (western coast). Therefore, total catch can be underestimated to be 5,000–6,000 t for eastern Kamchatka and 7,000–10,000 for western Kamchatka for 1931 and 1933. After 1986, data on the Russian catch were taken from the TINRO-Centre (Vladivostok) archive, and verified with data in the NPAFC annual reports and statistical yearbooks. All salmon catch values in this report are given in metric tons (t).

To compare trends in pink salmon catch dynamics for odd- and even-year pink salmon broodlines, the abundances were analyzed separately, which makes it possible to standardize the differences in absolute values of stock abundance. In our study, trends in catch dynamics for pink salmon were calculated as the arithmetic difference of the "expected" catch calculated as the mean value of the four previous years in the odd years or even years and the actual

catch. These methods of calculation were applied to reduce noise and provide a clearer picture of trend dynamics.

$$C_{exp\ 2004} = (C_{act\ 1996}+C_{act\ 1998}+C_{act\ 2000}+C_{act\ 2002})/4$$

$$D_{2004} = C_{act\ 2004} - C_{exp\ 2004},$$

where $C_{exp\ i}$ is "expected" catch for the corresponding year; $C_{act\ i}$ is actual catch for the corresponding year; and D_i is the deviation of actual catch from the "expected" catch in the corresponding year.

Variability in the catch data deviations (difference from the mean value, 86,568 t in 1956–2004) was also analyzed for the Russian coast to estimate its relationship to the world ocean heat content data (Levitus et al. 2005). The deviation graph has the same form as a graph of the values themselves and is conveniently used for the comparison with the data series, which include both negative and positive values. Increments (in conventional units) of pink salmon catch deviation were calculated to identify any hidden periodicity in salmon abundance under the influence of factors unrelated to the ocean heat content. The numerical significance of the catch data deviation was divided into the arbitrarily-selected number 14.5; the numerical significance of the ocean heat content (in 10^{22} J) was subtracted for each year from 1964–2004. We are aware of the approximateness of these values based on these rapid calculations.

Analysis of moving averages is traditionally used to examine long-term trends that may be masked by short-term factors, in particular, annual variability (Pyper and Peterman 1998; Wertheimer et al. 2001). However, the main objective of this study is variability in pink salmon abundance rather than a general examination of a long-term trend. This objective determined that we study the trends in variability on a medium and long-term scale.

Data on the average annual values of the Wolf numbers, which characterize solar activity, were acquired from the website of the National Geophysical Data Center of the US (ftp://ftp.ngdc.noaa.gov/STP/SOLAR_DATA/SUNSPOT_ NUMBERS). Spectral (Fourier) analysis for the recognition of dominant periods of variability in the data series was conducted using STATISTICA software. The Tukey window was used for evaluating spectral density.

RESULTS

The smoothed curve of the pink salmon catch series in the North Pacific is sinusoid with two highs and one low (Fig. 1). Two periods with relatively high levels are separated by years of low abundance (approximately, from the mid 1940s to the mid 1970s). This distribution has been associated with a periodicity in salmon productivity with a return period of 50–60 years (Beamish and Bouillon 1993; Chigirinsky 1993). However, the increase in salmon catch since they were first exploited was undoubtedly dependent

on growing market demands, technical progress in harvesting technologies and storage methods. Thus, the average annual catch of Pacific salmon in Aniva Bay was only 160 t in 1876–1902 and increased up to 13,670 t in 1907, following a drop in catches on Hokkaido Island, to satisfy the need for Japanese exports (Antonov 2005). In such periods of gradual increases in catch value, the 2-year cycle of catches in even and odd years was not usually observed. Therefore, it is difficult to judge whether these catch values reflect the level of the stock abundance, and, further, the length of time these periods of the high and low stock abundance last, and the amplitude of their fluctuations. Comparatively high catch values of Pacific salmon in Aniva Bay were observed until 1912, decreasing thereafter. In some other regions, exploitation rates during initial periods are known to be extremely high, where pristine fish stocks are newly fished by an already developed fishery. Such initial dynamics occur in other fisheries including 'fishing up' to some critical level, which is followed by a decline related to deterioration of fish stocks.

It must be emphasized that overharvesting could be not only a result of growing fishery pressure but also of stable fishery efforts toward a deteriorating salmon stock caused by the effect(s) of natural factors. When environmental conditions are unfavorable for fish reproduction, overfishing can be especially harmful. In the same way, pink salmon catch growth since the early 1970s could be related to stock conservation and artificial propagation (i.e. hatcheries) under favorable environmental conditions. All these circumstances could blur the natural duration of periods of high and low stock abundance.

Catch dynamics differed slightly on the North American and Asian sides of the Pacific (Fig. 1). Comparison of cumulative curves, which express the increasing sum of the deviations of the annual catch values from the long-standing average, revealed a close coincidence of pink salmon catch dynamics on both the Asian and North American sides of the Pacific (Beamish and Bouillon 1993; Chigirinsky 1993). Further, for the second half of the 20th century, catch variability on the Asian coast matched that on the North American side, but with some shift in extreme points. The best correlation with the North American catch histogram occurred on a twelve-year cycle, when segments of 1957–2001 for the Asian side and 1945–1989 for the North American side are compared ($r = 0.60$, $p < 0.001$, $n = 45$). It is possible that this was related to a gradual change in the environment and pink salmon stock conditions associated with water circulation in the North Pacific, i.e. from the North American coast to the western Bering Sea coast of Kamchatka, and then, to the western Kamchatka coast and Sakhalin and the Kuril islands. Many hypotheses concerning pink salmon dynamics emphasize how natural and anthropogenic factors affect salmon stock conditions and how it is difficult to determine their significance.

Despite distinctions in absolute abundance of spawning
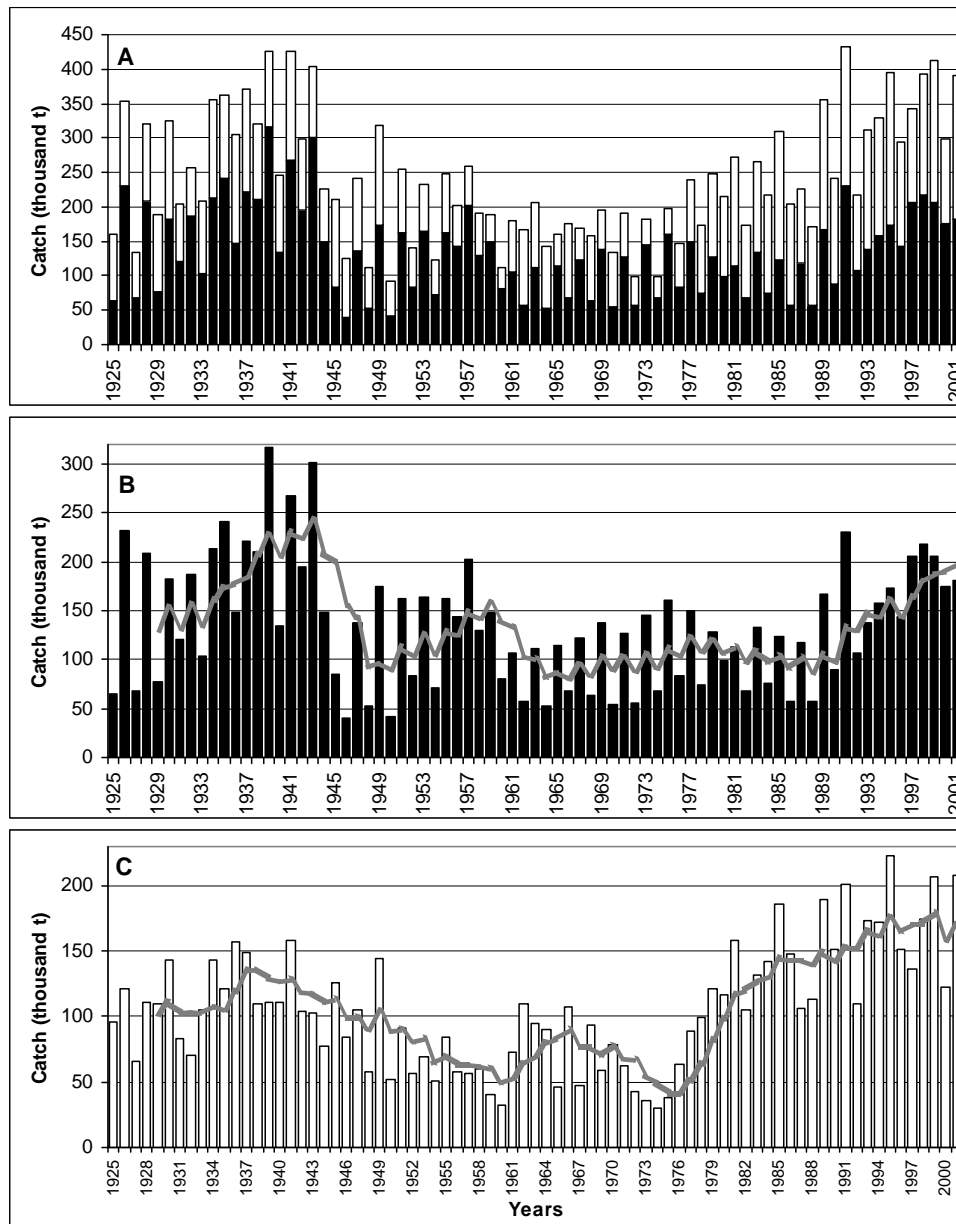
Fig. 1. Pink salmon catch (thousand tonnes) in the North Pacific. A: total; B: Asian coast; C: North American coast.

stock for the majority of stocks, the catch dynamics for the odd-year and even-year broodlines for the entire North Pacific have a moderate relationship ($r = 0.49$, $p < 0.005$, $n = 38$), especially for the last quarter of the 20th century after 1972 ($r = 0.82$, $p < 0.001$, $n = 15$). Summarized regional catch data equalized the difference between broodlines as in the average catch (272,721 t for odd years and 214,503 t for even years) and in extreme values (134,200–431,600 t for odd years and 92,900–392,800 t for even years). The standard deviations of the two data sets are equal ($F = 0.80$).

Most of regional groupings of pink salmon demonstrate considerably less similarity between catch data series in the even and odd years. The correlations are poor ($p > 0.05$) for regions such as the western and eastern Kamchatka coasts,

British Columbia, and the northern coast of the Sea of Okhotsk. Fishery statistics exist only for the odd-year broodline at the southern limit of pink salmon distribution on the US coast – in Washington, Oregon and California. On the Asian coast, pink salmon groupings from the Sakhalin-Kuril Islands region, eastern Kamchatka, and, to a lesser degree from Iturup Island, show the continued reproduction of the odd-year broodline (Fig. 2). The even-year broodline is maintained by pink salmon reproduction on the western Kamchatka coast and the southern Kuril Islands. On the American side, there are two extreme geographical regions: western Alaska and the states of Washington, Oregon and California that demonstrate the significant dominance of one broodline, while three other regions are characterized by similar values for
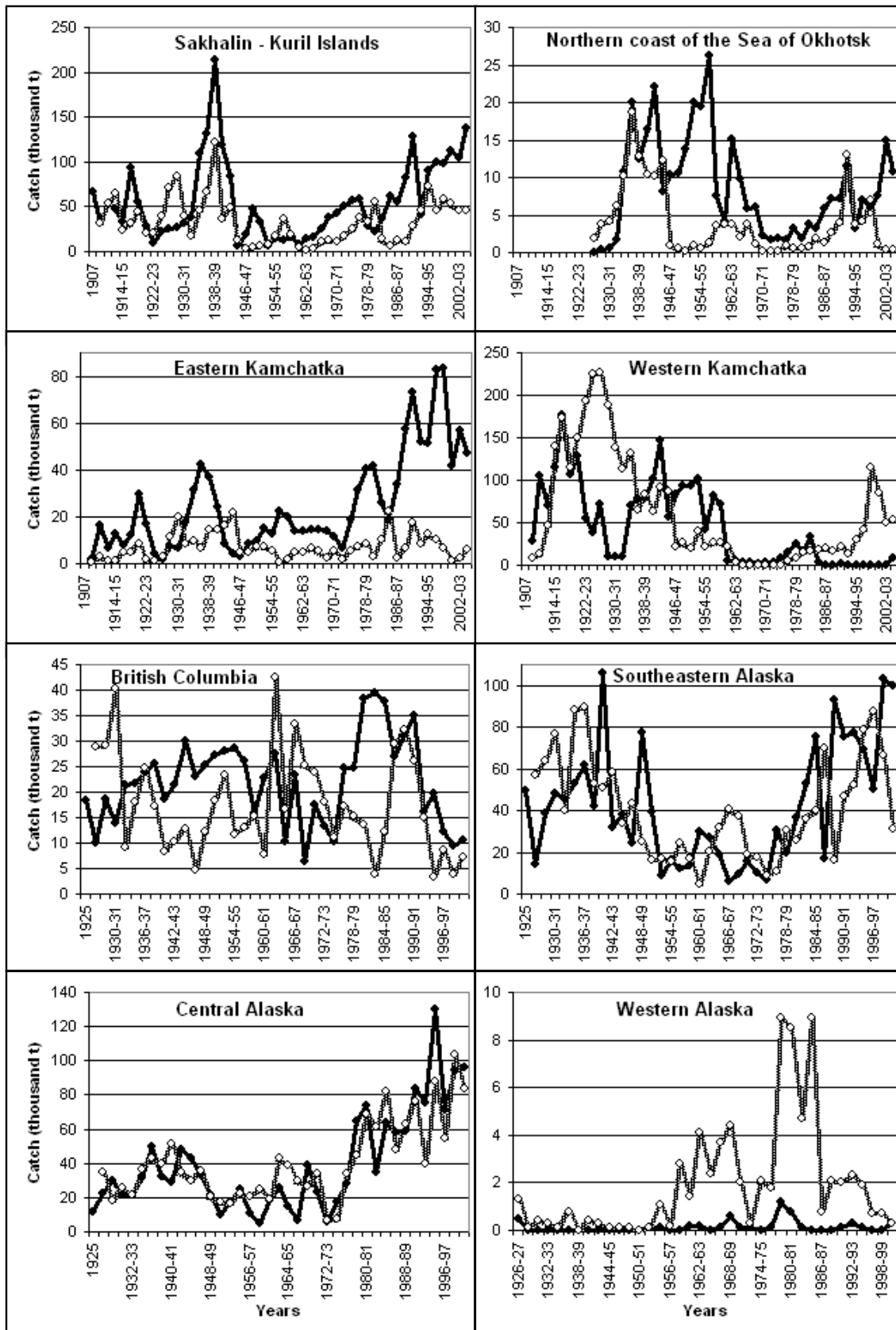
Fig. 2. Pink salmon catch (thousand tonnes) in the major fishery regions in the North Pacific. Black line and solid circles: odd-year broodline; gray line and open circles: even-year broodline.

annual pink salmon catch variability (Fig. 2). However, for the British Columbia coast, this similarity was evident after the 1990s, with the notable decline in catch values in the odd years as well as in the even years. This decline was unrelated to pink salmon abundance, which may be at historic high levels (Beamish et al. 2004). In southeastern Alaska, the years after 1985 were marked by a lack of similarity.

Catch dynamics of the entire pink salmon stock is more smoothed and similar on the scale of the whole Pacific Ocean or even on the scale of the Asian and American coasts separately than variations in the regional stocks. A dynamic equilibrium of even-year and odd-year broodline biomass on an oceanic scale appears because of the differences in the contribution of large regional pink salmon groupings to the total. Pink salmon stocks of western Kamchatka, western and central Alaska, and western Iturup Island contribute significantly to the total even-year broodline abundance. Eastern Kamchatka, central and southeastern Alaska and eastern Sakhalin Island stocks have contributed to the odd-year broodline abundance in recent years. Alternating the production of broodlines in the different regions demonstrates the unique life strategy of pink salmon, which is directed toward the maintenance of a sustainable level of reproduction for the species as a whole. This sustainable level likely corresponds to optimal exploration for food resources in the open waters of Pacific Ocean along feeding and migration routes and to the prevailing environmental and forage conditions.

Before 1934–35, the annual pink salmon catch level in Asia and in the entire North Pacific in even years exceeded the catch in the odd years. This phenomenon is explained by the larger contribution of stock from the western Kamchatka coast to the total Russian pink salmon catch in those years (56.0–75.2% in 1924–1934), where the even-year broodline still predominates (Radchenko 1998).

The trend in pink salmon catches in the North Pacific reveals a gradual decline of both broodlines until 1945–1946 (Fig. 3). Then, some stabilization occurred as shown by growth of the actual catch relative to the "expected" value, i.e. to the average for the four previous years. Deviations of actual catch from the "expected" catch have tended toward zero in the corresponding years. A relatively stable period lasted until 1973–1974. There was a period of growth up to 1987–1988, followed by one continuing until the present time. At the same time, catches were highly unstable. An alternating pattern of more or less productive generations occurred in both broodlines, at least during the last 10 cycles (or 20 years). The "saw tooth" catch deviations in recent years were not evident in previous years. Taking into consideration this high level of pink salmon abundance, it may be that a density-dependent factor was at play. However, inside the regional groupings, a regular alternating pattern was not observed in the catch values or the deviations from "expected" ones, neither for the even-year nor odd-year broodline (Figs. 2 and 4). If density-dependent factors affect pink salmon populations during the freshwater life stage, a more abundant generation of spawners could result in relatively less abundant progeny and *vice versa*. Variability of such abundance indices should first be evident at a regional level. Further, we suppose that the existence of density-dependent
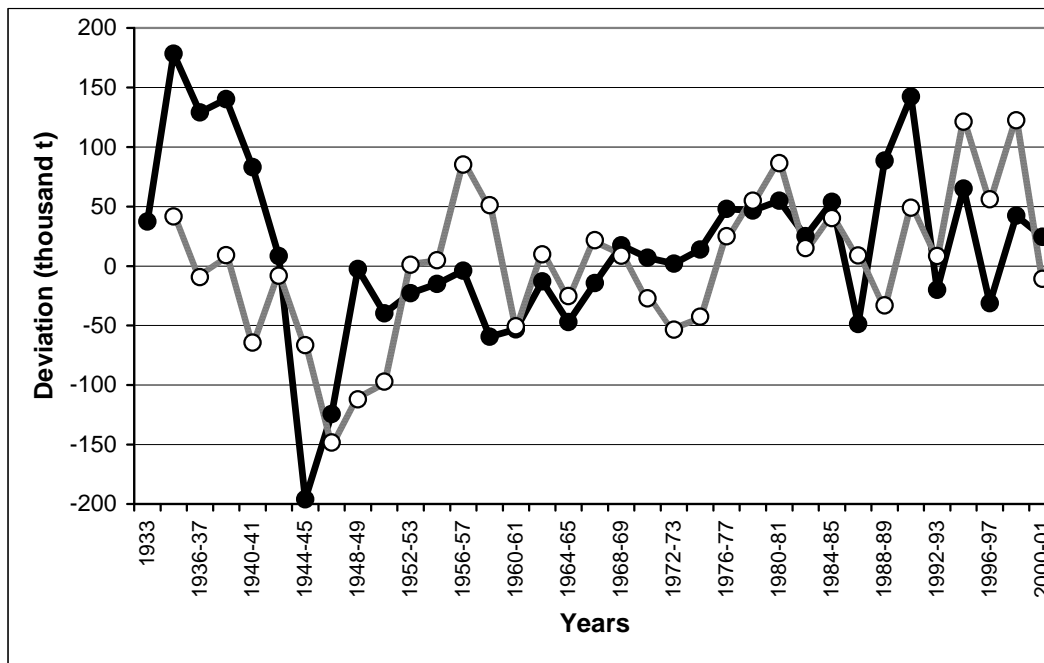
Fig. 3. Trends in pink salmon catch (thousand tonnes) in the North Pacific, 1933–2001. Black line and solid circles: odd-year broodline; gray line and open circles: even-year broodline. Explanations of trend calculations are given in the text.
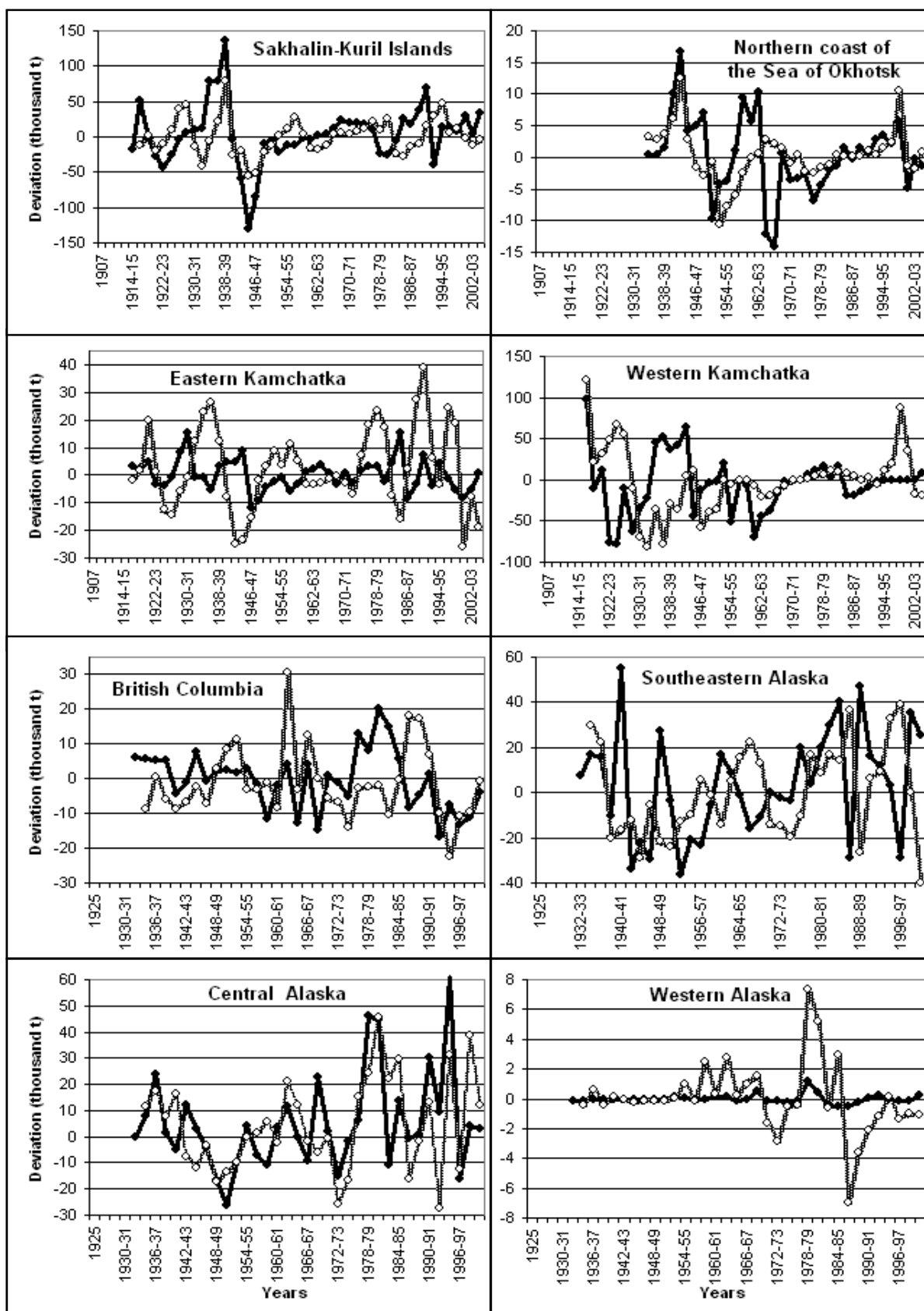
Fig. 4. Deviation of pink salmon catch (thousand tonnes) in the major fishery regions in the North Pacific. Black line and solid circles: odd-year broodline; gray line and open circles: even-year broodline.

factors that have an effect on the entire pink salmon population in the North Pacific Ocean affects salmon during feeding migrations, i.e. we assume that there is interference of stocks in the Pacific Ocean. These factors contribute to the overall marine survival of pink salmon.

For all the Russian coasts, total catch dynamics was closely matched in odd and even years (Fig. 5). One large distinction is the sharp decline that occurred during the odd years in 1923. It could be explained by a decrease in the pink salmon run to the Kamchatka Peninsula, the main location of the salmon fishery in Russia at the time. During the odd years of 1923–1933, the total Russian catch of pink salmon fell to 33,000–42,000 t, with the foreign catch falling below

to 58,033-86,527 t. Development of the pink salmon fishery on Sakhalin Island, where odd-year populations predominate, contributed to the increase in odd-year catches. The pink salmon catch increased sharply, reaching an absolute maximum value for the region (213,400 t in 1939), with the development of the Japanese fishery. Odd-year dominance of the interannual catch structure, which was formed during the 1930s, has been maintained for all the Russian coasts up to the present time. Despite this predominance in absolute values, catch data series for the odd-year and even-year broodlines demonstrate a strong correlation ($r = 0.79$, $p < 0.001$) since 1939.

Among the fishery regions on the Russian coast, a sig-
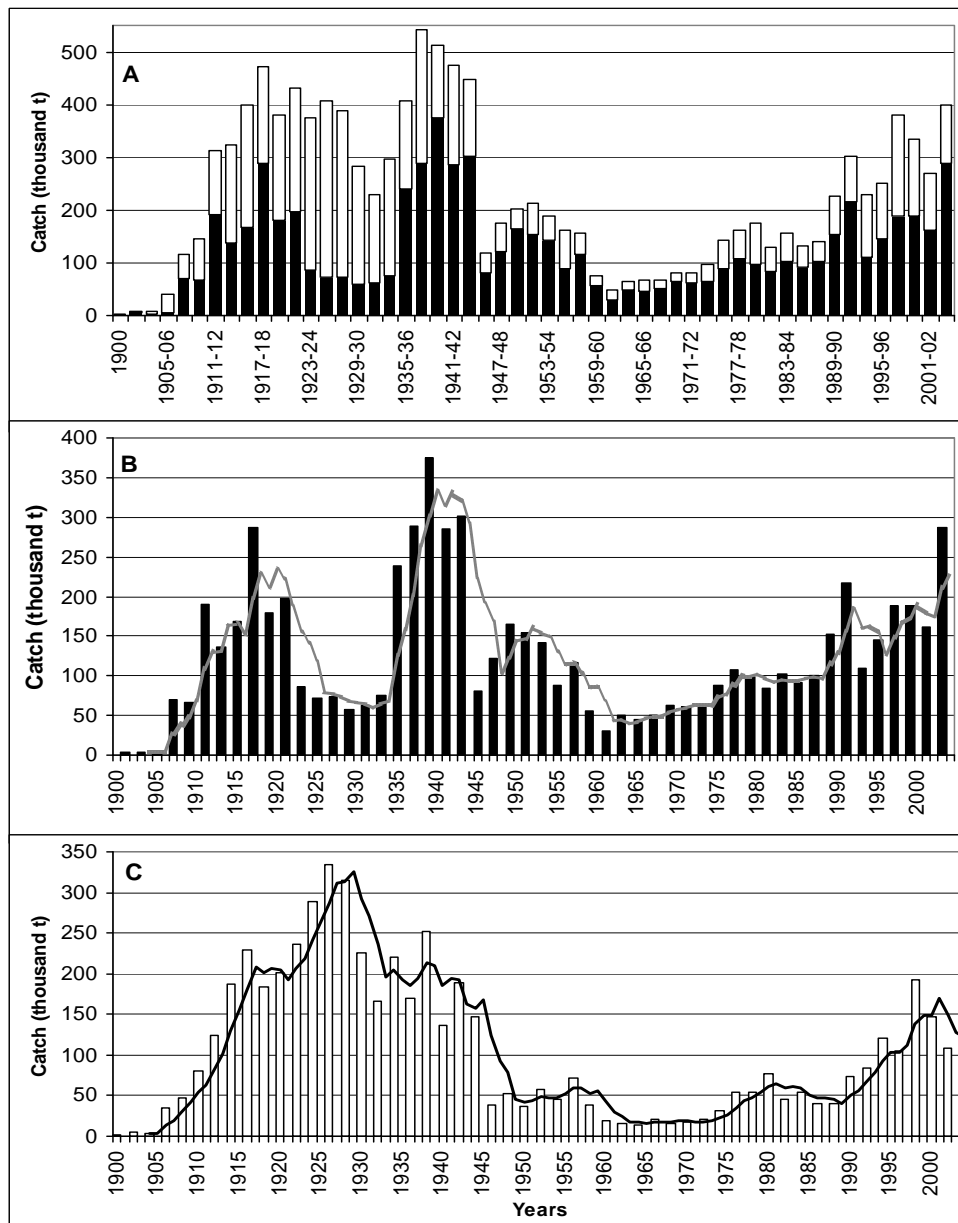
Fig. 5. Pink salmon catch (thousand tonnes) on the Russian coast, 1900–2004. A: total; B: odd years; C: even years. Three-year moving averages are presented on panels B and C by gray and black lines, respectively.
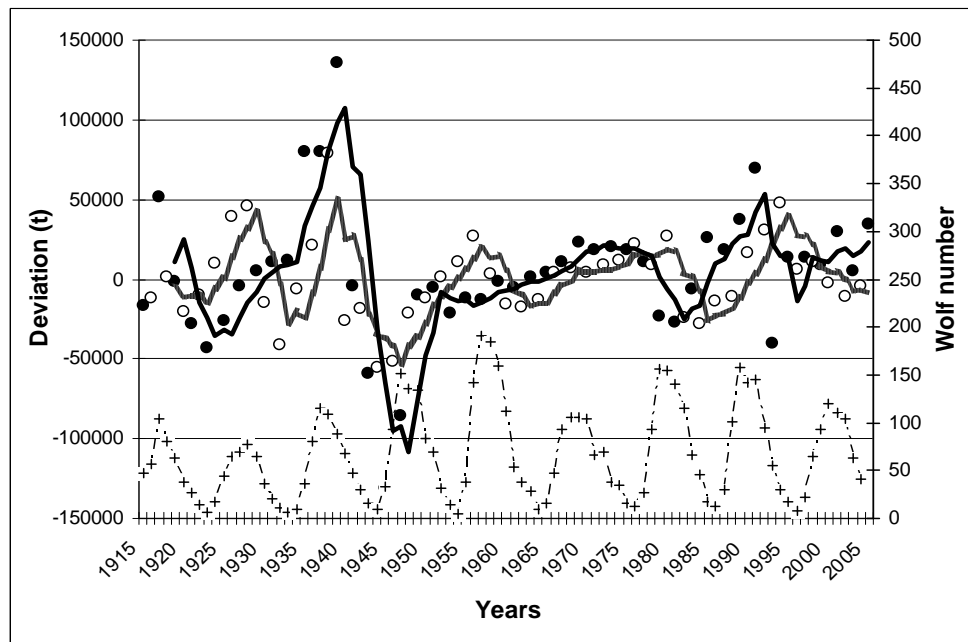
Fig. 6. Trends in pink salmon catch (tonnes) in the Sakhalin-Kuril Islands region, 1915–2005. Black circles: odd-year broodline; open circles: even-year broodline. Three-year moving averages are indicated by the black line for odd years and the gray line for even years. Solar activity is indicated by Wolf number (dotted line and crosses on the right-hand axis).
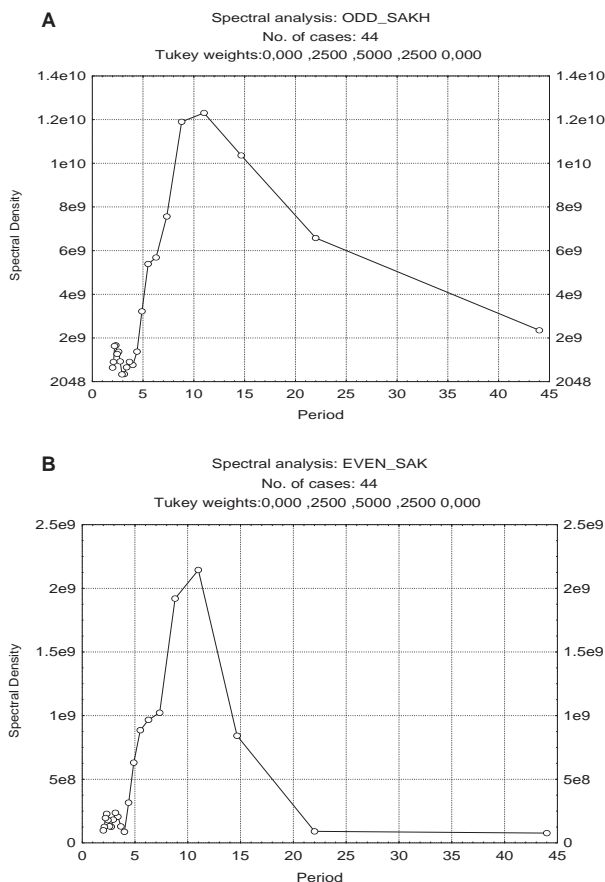
Fig. 7. Periodicity of deviations of expected catch for odd (A) and even (B) years in the Sakhalin-Kuril Islands region, 1915–2005.

nificant relationship between the annual catch data series (1908–2005) among the odd-year and even-year broodlines was found only for Sakhalin and the Kuril islands ($r = 0.59$, $p < 0.001$). On the North American coast, all three fishery regions of Alaska display significant relationships between catch data series (1926–2001) for both broodlines: $r = 0.34$, $p < 0.05$ for the southeastern coast; $r = 0.85$, $p < 0.001$ for the central coast; and $r = 0.66$, $p < 0.001$ even for western Alaska, where the pink salmon harvest value did not exceed 9,000 t in even years and 1,500 t in the odd years. However, it can be related, to some degree, to a longer data series for the Russian coast (n = 49 instead of 38 pairs of compared years).

When we compared trends in catch dynamics, a significant relationship was found for Sakhalin and the Kuril islands ($r = 0.48$, $p < 0.001$) and for the northern Sea of Okhotsk coast ($r = 0.40$, $p < 0.05$). On the North American coast, two fishery regions show significant relationships between data series of deviations of actual catch from the "expected" catch (1934–2001) for both broodlines: $r = 0.59$, $p < 0.001$ for central Alaska; and $r = 0.65$, $p < 0.001$ for western Alaska. The relationship was not significant for the southeastern Alaska and British Columbia coasts. Meanwhile, the trend curves are close to each other for southeastern Alaska (Fig. 4). More similarity can be found if we compare different time intervals separately. Thus, until the mid 1960s, the line which characterizes the change in the trend for the even-year broodline, preceded the line for the odd years by approximately one cycle. From the mid 1960s, the extreme points in the curve for the odd years were one cycle ear-

Table 1. Pearson's correlation coefficients (*r*) between normalized pink salmon catch data series and world ocean heat content, 1956–2004 (*n* = 49 for Russian coast; *n* = 46 for other areas). All relationships are statistically significant (*p* < 0.001).

	World ocean, 0-700 m	Northern Hemisphere, 0-700 m	World ocean, 0–300 m
Russian coast	0.59	0.58	0.63
American coast	0.48	0.53	0.57
Whole North Pacific	0.47	0.51	0.54

lier. From the late 1980s, the trend in the curves for both broodlines shows opposite changes, revealing the significant negative relationship for 1976–2001. We can suggest the occurrence of some prominent events, which affected the trend in pink salmon catch dynamics in the mid 1960s and 1980s. Local management changes likely strongly influenced the relationship. Pre-statehood federal mismanagement in Alaska led to pink salmon stocks being over-fished, resulting in a sharp reduction in catches at the beginning of 1960s (Heard 2001); an increase in the proportion of hatchery salmon in the general returns in 1980s (Hilborn and Eggers 2001) and management efforts for salmon stocks being undertaken in recent years, in particular, the establishment of a cumulative escapement goal for Prince William Sound by the Alaska Department of Fish and Game since 1934 (Wertheimer et al. 2001). All these factors may have blurred the trend dynamics compared to trends in other regions.

On the Russian coast, the deviations of actual pink salmon catches from "expected" catches for the odd-year and even-year broodlines were especially close for the Sakhalin – Kuril Islands region (Fig. 6). Coincidence of the trend curves for the odd-year and even-year broodlines was more apparent in the second half of the 20th century. Some sections of the curves, in particular those for the second half of the 20th century, completely coincided with the shift of curves relative to each other for four years (Fig. 6).

The comparison of the curves with the dynamics of the solar activity, expressed in Wolf numbers, showed that each of four 22-year cycles of solar activity includes the complete cycle of fluctuations in the catch dynamics trend. Spectral analysis revealed a clear 22-year cycle for trends for the even-year broodline (Fig. 7). Cycles appear unequal on the curve for the odd-year broodline. The longer cycles are separated by shorter ones and that is reflected in the results of the spectral analysis. The periodogram (by period) for the odd-year broodline is characterized by two contiguous maximums which correspond to cycles of 18 and 22 years. This may be related to the sharp decline in pink salmon catches on the Kamchatka coast in the 1920s and subsequent changes in the inter-regional ratios of catches.
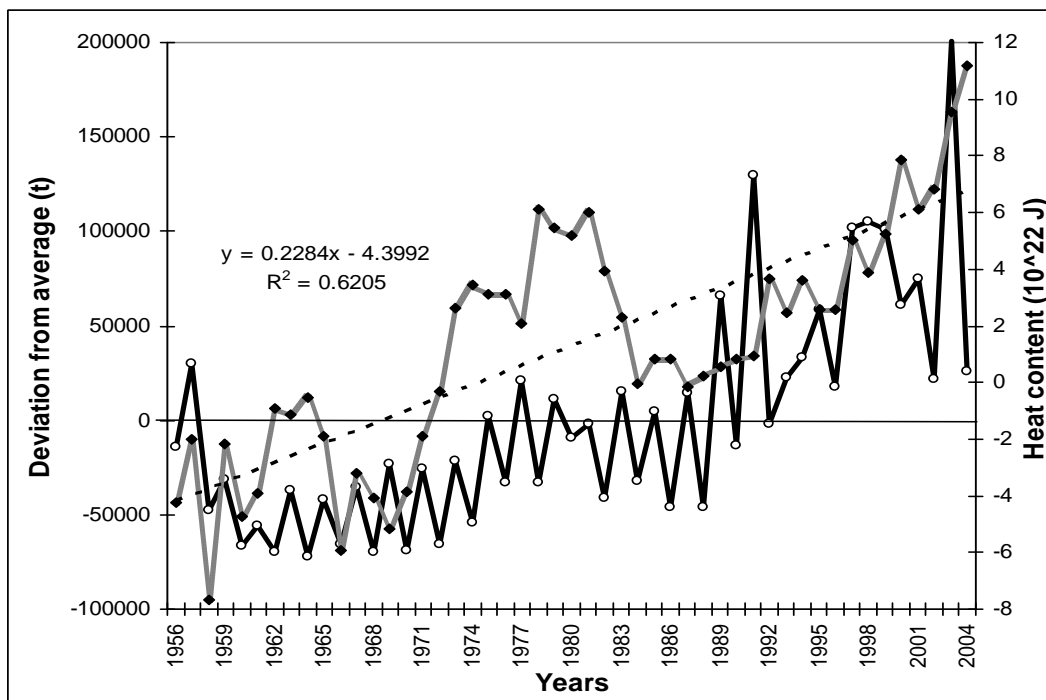
Fig. 8. Ocean heat content for the 0-700 m layer (gray line, solid diamonds, after Levitus 2005) and deviation from average of pink salmon catch (black line, open circles) on the Russian coast, 1956–2004. Trend in ocean heat content is indicated by the dashed line.

Another recognizable dependence of pink salmon catch dynamics on global physical factors was recently found. Pink salmon catch dynamics on the Russian coast correlate ($r = 0.59$, $p < 0.001$) with the increase in yearly world ocean heat content for the 0–700-m layer (Levitus et al. 2005). Assessing the statistical significance of other relationships shows that correlation coefficients do not change notably when data are replaced with ocean heat content data for the Northern Hemisphere only ($r = 0.58$) and for the upper 300-m layer ($r = 0.63$). Relationships are also significant for the total pink salmon catch in the North Pacific and on the North American coast (Table 1). It can be expected that the dependence is rather general and reflective of the integrated impacts. It is impossible to compare catch data for specific salmon populations and heat content at the location of its feeding and migration route. The limitation of ocean heat content data by a sample of observations for the Pacific Ocean and Northern Pacific weakens relationships for all three regions (Table 1). However, correlations improved with the restriction of ocean heat content data to the thinner, upper ocean layer, closer to the habitat of Pacific salmon.

The graph of the pink salmon catch deviations on the Russian coast (1956–2004) varied similarly to the graph of yearly world ocean heat content for the 0–700-m layer (Levitus et al. 2005). The trajectories approximating pink salmon catch and ocean heat content data are rather flat (Fig. 8). Relationships between catch dynamics and general ocean heat content are stable. Correlation coefficients change insignificantly with shifts of the data series each relative to the other

for one year. Furthermore, the highest correlation coefficients (0.65 instead of 0.63 for the Russian coast, 300-m layer) are seen with ocean heat content data series advanced by one year. This emphasizes that ocean heat content is determined by climate and synoptic conditions in previous years. For this reason, ocean heat content has shown a steady increase since 1956 in spite of some periodic variability (Levitus et al. 2005). The corresponding curve from Fig. 8 can be approximated by a straight line ($y = 0.2284x – 4.3992$) with $R^2 = 0.62$.

Pink salmon biological characteristics depend on stock abundance. In general, body weight and, to a lesser degree, length, of maturing pink salmon in the southern Okhotsk Sea and Pacific waters off the Kuril Islands in the summer of 1991–2003 changed in relation to different levels of their total biomass for the Sea of Okhotsk region (Radchenko 2001; Temnykh 2005). However, for particular cases, correlations between pink salmon body size and abundance level were both positive and negative in different regions, broodlines and time series (Temnykh 2005). As for juvenile pink salmon body weight, the smallest juveniles were sampled in the Sea of Okhotsk region after the largest downstream migration of 1993 (5.08 billion fish), whereas the largest ones were collected after the smallest downstream migration in 1994 (2.63 million fish). Before 1991–1992, the weight of spawners was, to a large degree, dependent on the size of migrating stock. According to coastal fishery data, it equaled 1.25 kg in the productive year 1991, and 1.50 kg in the unproductive year 1992. However, pink salmon broodlines that returned
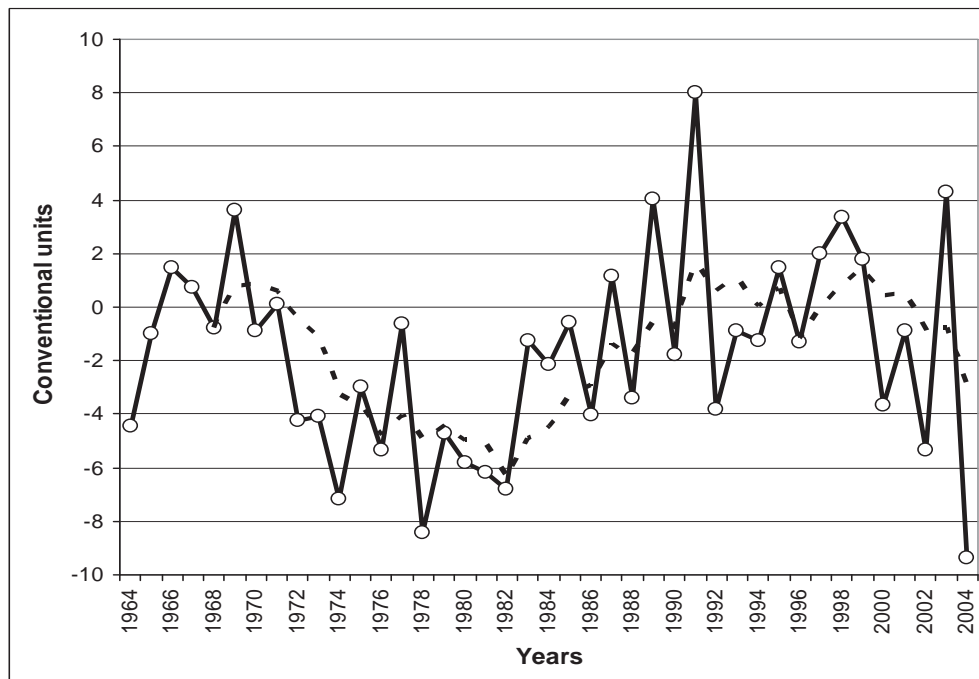
Fig. 9. Variability in increments (in conventional units) of pink salmon catch deviations after subtraction of ocean heat content for the 0-700 m layer, 1964–2004. Five-year moving averages are indicated by the dashed line.

to spawn in 1994–1997 support the correlation between the initial weight of juveniles entering the ocean and the final weight of spawners. Smaller spawners returned from the smallest outmigrants, and larger spawners from the larger ones independent of the total abundance of spawning stocks (Radchenko 2001).

DISCUSSION

Similarities in trends in abundance for the odd-year and even-year broodlines cannot be explained by biological effects of fish interaction because fish of both generations spend a brief time in the same waters simultaneously. Direct interrelation and genetic drift between broodlines seems to be negligible. Distinctions between the lines are emphasized by significant differences in abundance levels in most fishery regions and by pink salmon hatchery production in northwestern Russia. It is noteworthy that the hatchery pink salmon population of northern Japan typically shows a biennial cycle in the magnitude of the spawning run and catch value, despite almost equal numbers of fry released in the odd and even years (Radchenko, 2001). The same situation has been observed in the Great Lakes in spite of notable changes in pink salmon life span and the age structure of their populations. Thus, an assumption could be made of the existence of some global factor determining conditions for pink salmon reproduction and survival, which, in turn, causes a response of both broodlines to periodic dynamics independent of differences between them.

Effects of these global factors seem to be interrelated. Goryainov and Shatilina (2003) identified significant relationships between the surface atmospheric pressure field dynamics in the region of the Southern-Asian Low and pink salmon catches a year later. It is known that the Southern-Asian Low determines the intensity of monsoon circulation above the Far East, which, in turn, influences a series of factors, which limit pink salmon abundance during early developmental stages. Nevertheless, the strengthening of the relationships between the salmon catches and the pressure field above the regions along salmon feeding and migration routes was observed in vicinities of the Pacific High and Bering Sea Polar Trough locations in spring (Goryainov & Shatilina 2003). Regions of feeding migrations of separate regional groupings of pink salmon are distinct in the Pacific Ocean (Shuntov 1994). However, environmental factors continue to affect salmon at other stages of their life cycle and the relationships are not strong. Schumacher (1999) emphasized that in spite of the correlations of the dynamics of solar activity with different phenomena on Earth, the reason for hydrometeorological and biological changes does not lie in the dynamics of the solar energy flux, whose variability is insignificant (of about 0.1%, or 2 Vt/m^2 of the ocean surface). Nevertheless, many authors assume that such fluctuations can be sufficient for the initiation of changes in climatic conditions on the Earth's surface as a result of the variability of

temperature and the ozone content in the lower and middle atmospheric layers (Schindell et al. 1999; Haigh 2001; Patterson et al. 2004). The same atmospheric processes (variability of temperature and chemical composition) serve as basic components in the chain of signal transfer, initiated by the dynamics of the short-wave component of solar radiation (Häder et al. 2003). Ikeda (1990) assumed that the dynamics of solar activity generates decadal oscillations in the integrated system "atmosphere-ice-ocean" in the Northern Hemisphere. The relation of the solar activity was noted with the air temperature and the atmospheric pressure (Van Loon and Shea, 1999), with the ice cover (Hill and Jones, 1990), with the transfer of water masses and upwelling development (Guisande et al. 2004), and with stock dynamics of many pelagic fish species (Häder et al. 2003; Guisande et al. 2004; Patterson et al. 2004). Solar activity influences fish stocks both directly (through influence of ultraviolet radiation on the roe and fish larvae), and through the state of forage plankton resources, changeability in oceanological conditions, and other climatic parameters.

It can be suggested because of the dependence of pink salmon catch dynamics on the world ocean heat content that the gradual warming of the ocean surface layer as a non-cyclic climate component can influence salmon stock dynamics on a global level with demonstrated periodic variability. In general, pink salmon stocks in the North Pacific are characterized by a relatively high level of abundance driven by significant year-to-year growth since the mid 1970s and especially after the late 1980s. High stock abundance of pink salmon creates an expectation for a decline in the near future, which is generated by decadal scale variability in many global natural factors influencing fish stock conditions. The most frequent question asked about pink salmon dynamics is: When will the stocks begin to decline? Many researchers have tried to answer this question and proposed that pink salmon stocks would decline beginning in the mid 1990s (Chigirinsky 1993), the end of 1990s (Klyashtorin 1997), the first years of the 21st century (Radchenko 2001), and even for 2005 (Kaev 2005).

The effects of periodically varying physical factors were roughly assessed by removing the non-cyclic component. The analyses of pink salmon catch data increments after subtraction of the ocean heat content indices showed that these increments vary on (close to) a decadal scale (Fig. 9). A curve of five-year moving averages displays gradual growth from a minimal level in the early 1980s to the mid 1990s. In the first half of 1990s, the moving averages oscillated slightly near the maximum level followed by a gradual decrease since 1999. It can be concluded that the pink stock decline determined by periodically changing global factors has already happened, approximately in 1999. It could not be detected due to the positive effect of ocean heat content growth since the second half of the 1980s. Spectral analysis, applied to the pink salmon catch increments series, after subtraction of relative heat content units, shows a well-expressed bien-

nial cycle and supposes the existence of a 22-year cycle.

The positive effect of an increasing ocean heat content on pink salmon stock condition likely results in an increase in carrying capacity through stabilization of the food supply. Warmer waters provide favorable conditions for the survival and growth of most sub-Arctic zooplankton species. For example, crustacean growth rates have been found to be above average in warm conditions (Vinogradov and Shushkina 1987). This enhanced growth rate allows for a longer maturation period and spawning season. A meta-analysis of marine copepod species indicates that growth rate is positively correlated with increasing temperature and decreases in generation time allowing more productivity in warmer climates (Huntley and Lopez 1992). Calanoid copepod biomass was much higher in the eastern Bering Sea middle shelf during warm years (Smith and Vidal 1986), likely due to higher growth rates. These findings suggest that ocean water warming enhances ecosystem productivity from the lower trophic levels, particularly for planktonic crustaceans, which play a significant role in the pink salmon diet.

Besides food supply stabilization, one more critical feature of the pink salmon life cycle can be positively influenced by an increasing ocean water heat content. It is well known that the high mortality rate of pink salmon outmigrants occurs in the inshore waters in years of delayed seasonal water heating (Karpenko 1998). Formation of seasonal groupings, or races, is inherent in pink salmon of both broodlines (Kaev 2005). In the Sakhalin-Kuril Islands region, three of them are selected: "spring" Japan Sea grouping, "summer" (or early) and "autumn" (or late) oceanic races (Gritsenko 1981; Kaev 2005). An increase of the "summer" oceanic grouping portion occurred in the last few years. This grouping migrated earlier to the spawning grounds, and its outmigrants migrated to sea earlier.

A significant increase in juvenile pink salmon numbers in the offshore Sea of Okhotsk occurred in 1993 and again in 1999 despite the outmigrants' abundance remaining practically the same (Radchenko 2001). This increase in juvenile pink salmon survival correlates with the increased ocean heat content. Kaev (2005) related the increase of the "summer" oceanic grouping to the lower survival of the "late" race and expected changes in total stock abundance. However, it could be related to the increase in total pink salmon abundance. In 2005, the coastal pink salmon catch in the Sakhalin – Kuril Islands region reached 137,747 t exceeding the previous record of 1991 (128,333 t).

Observations on body weight dynamics lead us to the following conclusion: pink salmon body weight can serve as an index of marine life period success and effects of density-dependent factors but only for generations under the same environmental conditions. For the Sea of Okhotsk region, pink salmon stocks experienced some notable changes in the marine environment after 1991–1992. For the southwestern Bering Sea, it occurred slightly earlier. We can see a clear relationship between outmigrants' body weight and numbers after 1988, but not for all examples (Karpenko 1998). Pink salmon body weight may also depend not only on certain growth conditions, which are determined by the food supply and the hydrological environment. This can be related to the complicated stock structure of the regional pink salmon groups, specific peculiarities of regional stocks as were observed for the Sea of Japan pink salmon (Temnykh 2005). Seasonal races and ecological groupings have preferred development in different years that defines average size dynamics in a specific region, as the "summer" oceanic grouping for the Sakhalin and Kuril Islands area, complicating interpretation of body weights.

CONCLUSIONS

Pink salmon abundance and biological dynamics are complex. Trends in abundance of pink salmon stocks are determined under the influence of global physical factors that can be both periodic and non-cyclical. The solar activity dynamics and increases in ocean heat content play significant roles in this cumulative effect. In this aspect, data for ocean wintering of pink salmon have critical importance for future understanding of Pacific salmon dynamics.

Odd-year and even-year pink salmon broodlines reveal a recognizable relationship in abundance trends in the majority of fishery regions, independent of differences in absolute abundance between them. The existence of a strictly determined response of both broodlines to the periodic dynamics of some global factors, which determine the conditions of pink salmon reproduction and survival, can be regarded as the main cause of the relative permanence of the biennial cycle in the size of spawning runs, catch and escapement.

In general, pink salmon stock abundance in the North Pacific Ocean can be regarded as close to the historic maximum. However, there are grounds to expect that this level will be maintained in the near future in connection with the positive influence of increases in ocean heat content.

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Possible Causes and Effects of Shifts in Trends of Abundance in Pink Salmon of Southern Sakhalin and Iturup Islands

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Abstract: Data on the abundance of spawning pink salmon (*Oncorhynchus gorbuscha*) are presented for rivers of southern Sakhalin Island and Iturup Island. Fluctuations in abundance are more dependent on marine survival than on the abundance of fry migrating downstream. This is explained by the favorable spawning conditions in small rivers with dense aggregations on the spawning grounds. We found stable long-term trends in changes in abundance, fish length and the seasonal dynamics of spawning migrations. These trends suggest an important role for climatic-oceanological cyclical processes in pink salmon stock dynamics.

Keywords: pink salmon, Sakhalin Island, Iturup Island, spawning migration, abundance, body length, reproduction

INTRODUCTION

Many researchers consider density as an important factor when explaining decreases in body size and female fecundity, increases in age-at-maturity and delays in timing of the Pacific salmon spawning migration of abundant year-classes (Yefanov and Chupakhin 1982; Ishida et al. 1993; Welch and Morris 1994; Bigler et al. 1996; Volobuev and Volobuev 2000). However, not all the indices mentioned above fall into this pattern on a consistent basis. For instance, a decline in catches and body size in pink salmon (*Oncorhynchus gorbuscha*) was observed during the 1970–1980s on the Russian coast of the Japan Sea (Gavrilov and Pushkareva 1996; Temnykh 1999); and, in contrast, their synchronous increase in some areas of the Okhotsk Sea coast in the late 20th century (Nagasawa 2000; Temnykh et al. 2002; Kaev and Chupakhin 2003). These examples suggest that a variety of changes occurs in Pacific salmon stocks in different years.

To understand the patterns of these natural processes it is important to study salmon stocks in different regions. The pink salmon was selected for this study because it is the most abundant species of Pacific salmon. Further, the intensive pink salmon commercial fishery facilitates a higher degree of accuracy in determining the size of individual year-class stocks and the dynamics of spawning runs. Among Pacific salmon, the pink salmon shows the greatest fluctuations in abundance, which is related, primarily, to its short life cycle (two years). From July through October these fish migrate from the sea to rivers for spawning. During spawning they lay eggs in redds, which are located at 20–30 cm depth. Hatching and larval development take several months. Pa-

cific salmon progeny at early developmental stages are comparatively well protected on spawning grounds. As a rule, during a spring flood the fry begin migrating downstream. These processes take place from late April to early July. During the first summer, juveniles feed in the Okhotsk Sea and then move into the Pacific Ocean in late autumn to overwinter. The next summer, beginning in July, mature pink salmon return to natal rivers to spawn, thereby completing the cycle. Thus, fluctuations in abundance reflect the influence of environmental factors mainly during the period when pink salmon are adapting to their marine habitat. All of these factors make the pink salmon an attractive subject for studying fish abundance (Nikolsky 1974). Here we have analyzed changes in reproduction, abundance, and size composition of pink salmon in different spawning areas of the Sakhalin-Kuril Region.

MATERIALS AND METHODS

The three largest Sakhalin-Kuril pink salmon groups, each with very different spawning areas, both climatically and hydrographically, were chosen for this study. Quantitative data on fry migrating downstream, the abundance of spawners, and several biological indices have been collected during 30–35 years for fish from each area.

The number of wild fry migrants was calculated based on fish sampled in fyke nets (Volovik 1967) in the following rivers: the Bakhura and Dudinka rivers located in the southeastern Sakhalin coastal zone; the Bystraya (tributary of Lutoga River), Kura and Sheshkevich rivers located in the Aniva Bay coastal zone; and the Rybatskaya and Olya rivers

located on Iturup Island. The number of wild smolts in other rivers of these regions was estimated based on the number of pink salmon entering spawning grounds and the average number of fry migrants from one female in the above sampled rivers. Data on the quantity of hatchery fry released were taken from the statistical reports prepared by the staff of "Sakhalinrybvod" (Sakhalin Basin Department for Reproduction of Water Biological Resources) on fry releases from salmon hatcheries.

The number of returns of pink salmon was determined as the sum of individuals caught during commercial fishing and at fish weirs, and those migrating up rivers to spawn. The number of spawners on spawning grounds was counted by on-foot observations when there were maximum pink salmon concentrations in rivers (mainly the first half of September). Fish have been counted in this way in 13 rivers on the southeastern coast of Sakhalin Island (spawning grounds make up 67% of the total area of these rivers), in 21 rivers on the Aniva Bay coast (74%, respectively), and in 11 rivers on Iturup Island (73%, respectively). Numbers of pink salmon in other rivers of these regions were calculated based on the ratio between the spawning areas and the average number of fish per 1 m² in the studied rivers. The survival index of pink salmon was calculated as the ratio of returned adults to the total number of fry migrants. This calculation was based on the assumption that pink salmon catches from coastal waters reflect, in general, the reproduction level of the local pink salmon populations. High rates of straying of fin-clipped pink salmon and subsequent low recoveries of returning

adults (Rukhlov and Lubaeva 1980) were not seen when we studied recent data in more detail (Kaev and Chupakhin 2003; Kaev and Antonov 2005).

Biological analyses were done for fish from trap-net commercial catches and from beach-seine research catches in rivers. Usually one sample consisted of 100 randomly selected individuals. Biological analysis included determination of sex, standard body length and weight, and individual fecundity of 25–30 females from the sample. A total of 152 samples (13,938 individuals) was collected from 1979–2004 on the southeastern Sakhalin coast, 316 samples (28,379 individuals) from 1976–2004 in Aniva Bay, and 255 samples (26,008 individuals) from 1967–2004 at Iturup Island.

To study the long-term changes in fish abundance and biological indices, the collected materials were organized in such a way that the data used for analysis were obtained by the same methods in all observation years. This applies to determining the abundance of fry migrants and adults, the mean values of fish length and weight, and the fecundity of females from individual year-classes (Kaev and Chupakhin 2003; Kaev et al. 2004b). To study the timing of the pink salmon prespawning migration in coastal areas we used only data from trap-net catches (passive fishing gear). Differences in the timing of the spawning migration for different year-classes were estimated by the dates when half of the fish were caught.

Standard statistical methods were used (Plokhinsky 1970). Trend lines were calculated based on 4-year moving averages, because the interannual changes in pink salmon abundance and biological indices are related to their two-year life cycle. While studying long-term relationships among pink salmon abundance, migration timing, and fork length, all the calculations were performed using the original data.

The following symbols are used in the text: *M*, mean; *SD*, standard deviation; *CV*, coefficient of variation; *R*, coefficient of correlation; *p*, statistical significance; *N*, sample size.

RESULTS

Southeastern Sakhalin Island, the Aniva Bay coast and Iturup Island are relatively small areas of the Okhotsk Sea coast (Fig. 1). However, the pink salmon catches in these areas comprise more than half (55%) of the total Russian pink salmon catch in the Okhotsk Sea. The average annual catch of pink salmon in 1995–2004 totaled 19,211 tons in southeastern Sakhalin, 13,446 tons in Aniva Bay and 25,133 tons in Iturup Island. Further, reproductive conditions differ in these areas, despite their relatively close geographic proximity. Southeastern Sakhalin is distinguished by its cold winters. Most of the Aniva Bay rivers are concentrated on its western coast which has the warmest winters on Sakhalin Island. Iturup Island, which is located in the southern part of the Large Kuril Ridge, has even seasonal dynamics
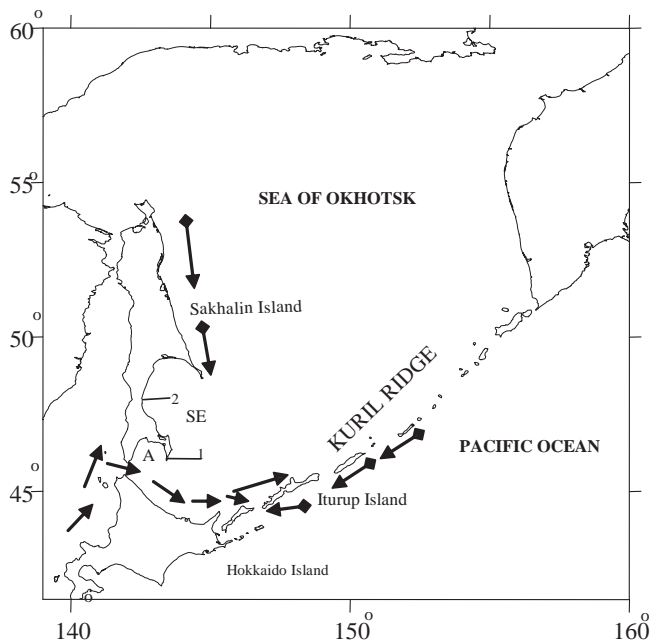
Fig. 1. Study regions for pink salmon. A, Aniva Bay; SE, southeastern coast of Sakhalin Island between Cape Aniva (1) and Cape Tikhiy (2). Single headed arrows = warm currents; two-headed arrows = cold currents.

in air temperature and snowy winters with frequent thaws. While Sakhalin rivers are almost completely covered with ice in winter, the Iturup rivers, as a rule, freeze only during periods of low discharge. The rivers on Iturup are short; the upper spawning grounds in the longest ones are located only 8 to 10 km from the mouth. In southeastern Sakhalin, the majority of pink salmon also spawn in the comparatively short rivers with the upper spawning grounds located only 10 km from the mouth. On the Aniva Bay coast, pink salmon spawn mainly in rivers that are up to 30 km long or more.

The early marine period in the juvenile pink salmon life cycle has different characteristics in each area. The coastal zone of southeastern Sakhalin is under the influence of the cold Eastern Sakhalin Current. Aniva Bay's hydrological regime is influenced by the cyclonic circulation that results from the interaction of the cold Eastern Sakhalin Current and a branch of the warm Tsushima Current. The coastal conditions of Iturup Island are determined by the interaction of several currents that form a local frontal zone with high productivity (Naletova et al. 1997).

Aniva Bay (Kaev et al. 2004a; kaev@sakhniro.ru, unpublished data, 2004)

In Aniva Bay, pink salmon spawn in 60 rivers with a total spawning area of 1.67 million m². During 1975–2003, from 0.3 to 6.93 million individuals (average 2.6 million), entered these rivers. The result of their spawning was from 26 to 486 million fry migrants (average 164 million). In addition, between 18 to 101 million hatchery fry (average 59 million) were released. Total spawning returns after a year in the ocean were from 0.5 to 34.5 million individuals (average 8.9 million). From 0.0 to 29.8 million of the spawning returns were taken in the commercial fishery. On average, pink salmon abundance during the observation years was almost three times as high in odd years (12.6 million individuals) than in even years (4.2 million individuals); however, variation in abundance in even years ($CV = 94.3\%$) was higher than in the odd years ($CV = 76.2\%$).

Southeastern Sakhalin (Kaev et al. 2004a; kaev@sakhniro.ru, unpublished data, 2004)

Pink salmon spawn in 29 rivers, with a total spawning area of 1.49 million m². In 1970–2003, from 0.4 to 10.6 million individuals (average 4.1 million), entered these rivers. A result of their spawning was from 35 to 1,230 million fry migrants (average 240 million). In addition, between 27 to 259 million hatchery fry (average 118 million) were released. Pink salmon spawning returns after a year feeding in the ocean were from 1.4 to 43.4 million individuals (average 16.1 million). From 0.4 to 36.4 million fish were taken in the commercial fishery. On average, pink salmon abundance during the observation period was almost twice as high in odd years (21.5 million individuals) than in even years (10.4 million individuals); however, variation in abundance in even years ($CV = 92.6\%$) was almost twice as high as in odd years ($CV = 50.7\%$).

Iturup Island (Kaev and Chupakhin 2003; Kaev et al. 2006)

On Iturup Island, pink salmon spawn in 87 rivers, but the majority of their spawning grounds (82%, or 600,000 m²) are concentrated in 54 rivers on the Okhotsk Sea coast. In 1970–2003, from 0.8 to 2.5 million individuals (average 1.4 million), entered these rivers. A result of their spawning was from 66 to 460 million fry migrants (average 210 million). In addition, between 62 to 215 million hatchery fry (average 134 million) were released. Spawning returns after a year in the ocean were from 5.9 to 32.1 million individuals (average 15.5 million). From 4.9–30.0 million fish were taken in the commercial fishery. On average, the variation in pink salmon abundance during the observation years was approximately equal in odd years (15.2 million individuals, 39.5%) and even years (15.7 million individuals, 41.4%). However, this does not necessarily mean that the change in the variation in abundance was small in both odd and even years. Until 1981, few differences between contiguous years were observed. Then from 1982–1992 mean pink salmon abundance was higher in odd years (21.4 vs. 11.4 million individuals). Since 1993 abundance has been higher in even

Table 1. Correlation coefficients for changes in abundance, escapement timing and fork length of pink salmon from different areas of the Sakhalin-Kuril region.

Area	Period	Abundance – Escapement timing		Abundance – Fork length	
		By the untransformed values	By the trend lines	By the untransformed values	By the trend lines
Aniva Bay	1975–2004	-0.19	0.10	0.08	0.80***
Southeastern Sakhalin	1975–2004	-0.04	0.01	-0.04	0.55**
Iturup Island	1967–2004	0.34*	0.56***	-0.28	-0.36*
	1975–2004	0.01	-0.23	-0.09	0.33

Note: Asterisks indicate the values of Fisher's criterion exceeding the critical values at 95% (*), 99% (**) and 99.9% (***) significance levels.
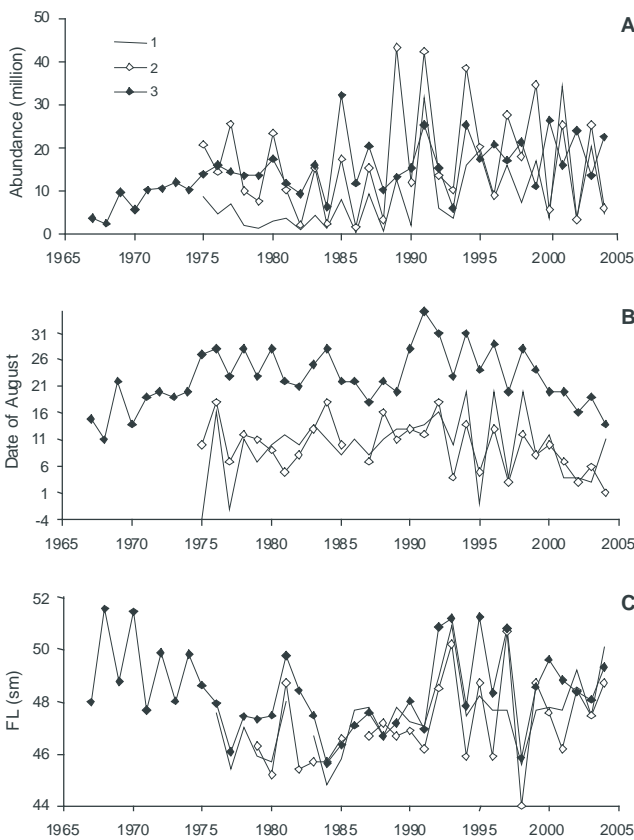
Fig. 2. Changes in abundance (A), escapement timing (B: date of the 50% capture) and fork length (C) of pink salmon from different spawning areas. 1, Aniva Bay; 2, southeastern Sakhalin; 3, Iturup Island.

Fig. 3. Dynamics of catches and changes in pink salmon fork length on the southeastern Sakhalin coast in 1994, 2000, and 2004. 1, male fork length; 2, female fork length; 3, daily catches.

years (23.4 vs. 13.6 million individuals).

Despite the differences in pink salmon abundance between odd and even years, periods of synchronous increase or decrease in indices such as abundance, escapement timing, and fork length are observed. Consider the changes in the Iturup fish which have the longest data record. An increase in abundance, delayed escapement timing, and a decrease in fork length were observed until the second half of the 1970s (Fig. 2). The 1980s were characterized by a decrease in abundance for the even-year-classes, whereas the abundance of the odd-year-classes remained the same, except for 1985, which had record levels of escapement (32.1 million). This resulted in a rise in the trend line in the mid 1980s. During the 1980s, pink salmon were smaller in size, and the migration timing of different year-classes did not vary significantly. Since the end of the 1980s an increase in abundance has been recorded, and, until the mid 1990s, returning fish were larger and they returned at later dates. Further, fish continued to be abundant and comparatively large but escapement timing began to shift to earlier dates. This became especially evident at the beginning of 21st century. As the result, the correlation between abundance and escapement timing was positive, and between abundance and fork length, negative.

However, correlation coefficients were low, except for the one characterizing changes in the trend lines for abundance and escapement timing (Table 1).

Changes in the same indices in the Aniva Bay and southeastern Sakhalin pink salmon differed from those for the Iturup fish only in details. For instance, in these regions the most noticeable decline in pink salmon abundance was in the 1980s, when a trend toward delays in spawning times began to appear, and fish were smaller in size, on average. A relatively strong, positive relationship was found only between the trend lines for fish abundance and fork length (Table 1). Two features should be taken into account when comparing correlation coefficients in the three study regions. First, the data record for Sakhalin Island is shorter; it begins during a decrease in abundance, but before the period of very low abundance in the 1980s. Correlation coefficients for Iturup fish, calculated for the same period, are close to the corresponding indices for fish from both regions. Second, after the abrupt decline in pink salmon abundance in 1993 in all regions, the even-year-classes began dominating in abundance on Iturup Island. On Sakhalin Island the high abundance of the odd-year-classes re-appeared. Despite this phenomenon, pink salmon abundance continued to be at a

comparatively high level and increased fish returns were re-corded. Simultaneously a trend toward shifting escapement timing to earlier dates was observed.

In our analysis, we took into account changes in pink salmon body length during the spawning run. Usually, a trend toward a gradual increase in fish size and changes in the ratio between male and female size are common. In the second half of fish run there is an abrupt increase in male size. As a result, compared to the first half of the run, males become larger than females. Such changes are shown for southeastern Sakhalin pink salmon during the beginning, middle, and end of the last period during which there was a shift in run timing toward earlier dates (Fig. 3).

When considering the long-term trends in changes in fish abundance, escapement timing and fish size (Fig. 2), the great differences in these parameters in contiguous years become important. To study these changes, the data were grouped according to the changes in abundance (increase, decrease, or no change, compared to the previous year). A rank "without changes" corresponded to parameters where changes did not exceed a statistical error of the mean value of the sample examined. Taking into account that the Kuril-Hokkaido even-year-classes and the Sakhalin odd-year-classes more often dominate in abundance, the data were compared in two ways. In the first approach we used the abundance of the stocks studied. In the second, we considered the regional abundance including pink salmon from eastern Sakhalin, the southern Kuril Islands and Hokkaido. We found no co-dependence using either approach to study changes in parameters (Table 2).

Prior to analyzing the data in Table 2, recall that the changes corresponding to the concept of the density-dependent regulation are reflected in either the delay (or acceleration) in the dates of migration timing and the decrease (or

increase) in fork length corresponding to an increase (or decrease) in abundance. Such changes have been shown only for the Iturup fish, for which the synchronous changes in escapement timing occurred in 57-62% of cases, and asynchronous changes in fork length in 59-62% of cases coinciding with changes in abundance. Similar changes between the fork length and abundance were recorded for pink salmon from southeastern Sakhalin in only half of the cases (52%). For the Aniva Bay fish such situations were seen less frequently (36-43%). Changes in escapement timing that were synchronous with changes in abundance were also not frequently seen in fish from Aniva Bay (25-29%) and southeastern Sakhalin (28-31%).

A reliable relationship between the number of pink salmon returns and number of spawners was found only in Aniva Bay (Fig. 4). There, the number of downstream fry migrants increased concurrent with an increase in the abundance of spawners on spawning grounds (Fig. 4). Quantitative dependence of pink salmon returns on the total number of fry migrating from rivers to the ocean was strong in all regions (Fig. 5). However, even in these instances the correlation coefficients were average, because the number of pink salmon returns is mainly determined by survival during the marine period. The same trend toward a decrease in survival index for both the highly abundant year-classes and less abundant fry migrants was observed in Aniva Bay and southeastern Sakhalin (Fig. 5). When analyzing the data in Table 3, we note the great importance of the marine period in determining the abundance of pink salmon returns. In all the regions, the periods with abundant pink salmon returns were characterized by high survival indices. This reflects a high level of survival during the marine period. It was only in Aniva Bay in 1995–1998 where comparatively high returns were related to an abundant fry harvest. Along with high

Table 2. Percent changes in pink salmon escapement timing and fork length (FL) in Aniva Bay, southeastern Sakhalin and Iturup islands in relation to species abundance in the study area (upper value) and in the broader region* (lower value) in contiguous years.

Changes in indices		Aniva Bay		Southeastern Sakhalin		Iturup Island	
Species abundance	Escapement timing and fork length	Escapemt. timing (n = 28)	FL (n = 28)	Escapemt. timing (n = 29)	FL (n = 25)	Escapemt. timing (n = 37)	FL (n = 37)
Increase or decrease	Synchronous with abundance	25 29	39 36	31 28	28 28	57 62	32 32
	Asynchronous with abundance	54 54	36 43	69 69	52 52	33 33	59 62
	Without changes	14 14	18 18	0 0	20 20	5 5	3 6
Without changes	With changes	7 3	7 3	0 3	0 0	5 0	3 0
	Without changes	0 0	0 0	0 0	0 0	0 0	3 0

*Pink salmon abundance on the eastern coast of Sakhalin, the southern Kuril and Hokkaido islands (Anonymous 2004).
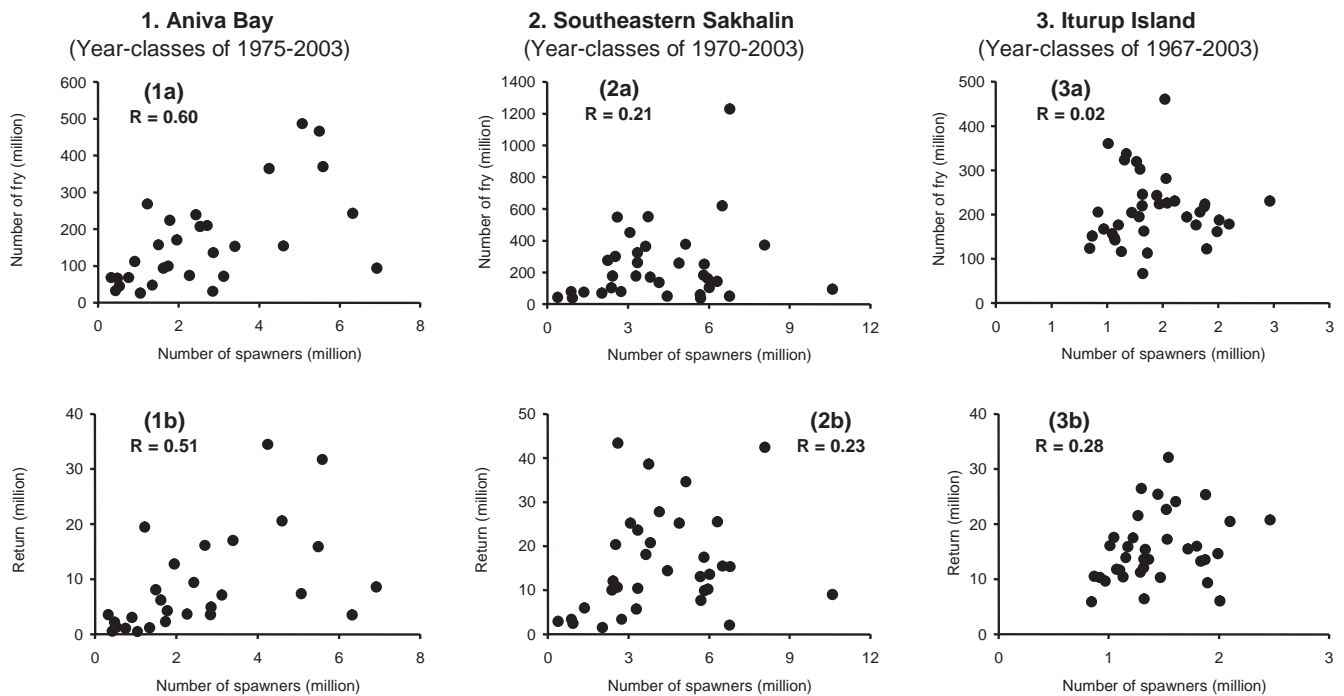
Fig. 4. Dependence of pink salmon fry migrants (a) and returns (b) on the number of spawners in rivers from different spawning areas.
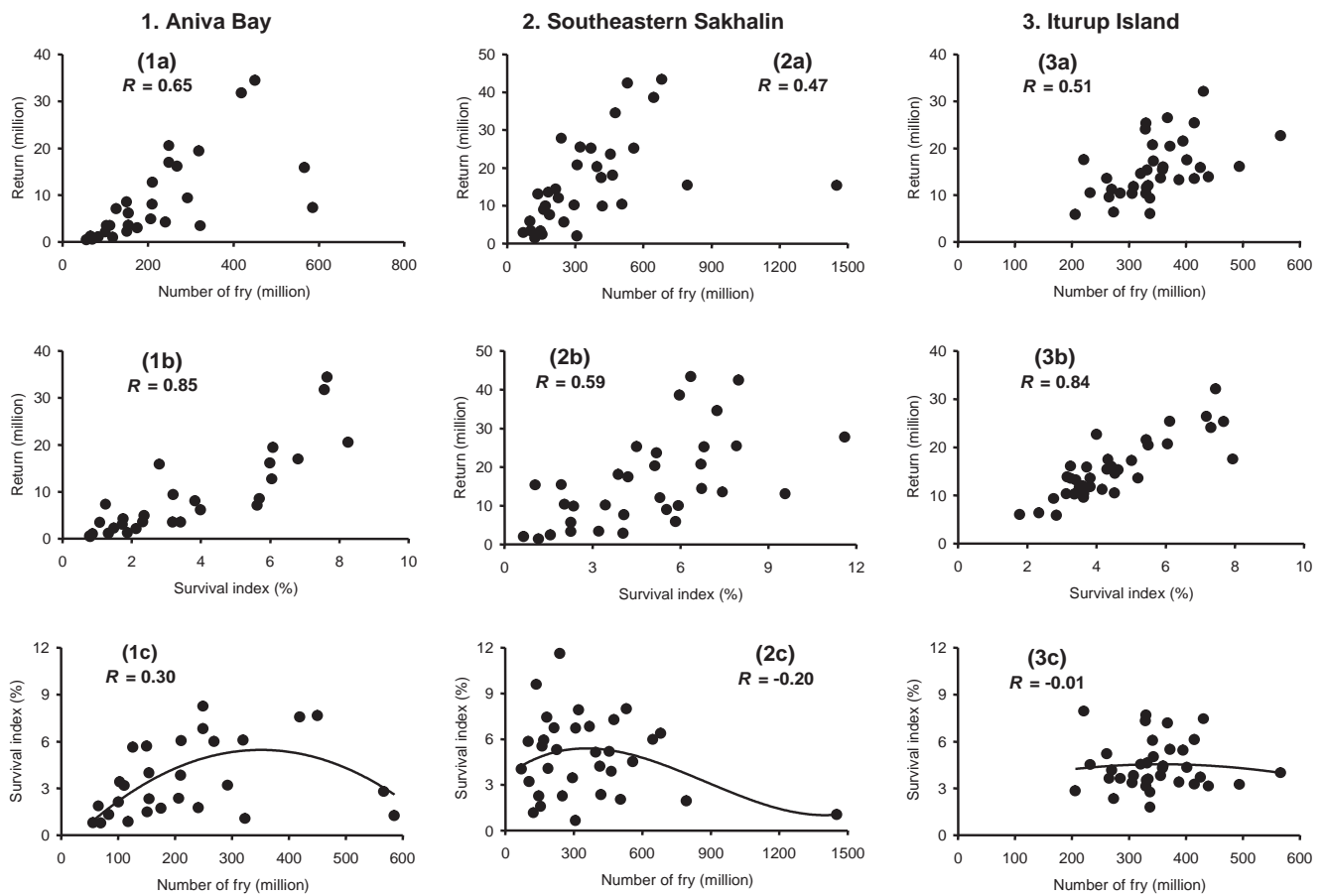
Fig. 5. Co-dependence of reproduction indices for pink salmon during the marine period in different spawning areas. (a) dependence of pink salmon returns on the harvest of fry migrants; (b) fish survival during the marine period; (c) dependence of pink salmon survival during the marine period on the harvest of fry migrants.

fish survival in the ocean, an increase in fry migrants was also correlated with increased pink salmon returns to Iturup Island in 1999–2002.

DISCUSSION

The data on the ratios among the abundance of spawners, number of fry migrants, and pink salmon returns illustrate the uniqueness of each of the regions considered here. First, we note the weak dependence of the abundance of fry migrants on the abundance of their parents in regions with very dense aggregations of fish on the spawning grounds in the Iturup rivers (average 2.11 ind/m^2) and southeastern

Sakhalin (average 2.76 ind/m^2). In southeastern Sakhalin, especially in the large rivers, there are reserves of unused spawning grounds, which, when fully occupied in particular years, leads to an increase in the abundance of downstream fry migrants. As a result, the importance of spawners' abundance in determining the abundance of fry migrants in this region (Fig. 4) is greater than that in the Iturup Island rivers (Fig. 4). By contrast, in the Aniva Bay rivers, where the number of spawners per area of spawning grounds (average 1.56 ind/m^2) is the lowest, the number of fry migrants depends more strongly on the number of their parents (Fig. 4).

Patterns of changes in year-class marine survival are different in each of the study regions. If we proceed from

Table 3. Mean abundance (in millions) of pink salmon adults and fry in different Sakhalin–Kuril regions for year-classes, according to years of fish spawning.

Years of spawning	Abundance of adult fish in rivers	Abundance of fry migrants*	Abundance of returns	Survival index (%)
Aniva Bay				
1975–1978	1.78	133.7 (38)	3.36	2.51
1979–1982	0.85	133.7 (25)	2.50	1.87
1983–1986	1.35	157.0 (28)	4.60	2.93
1987–1990	2.42	221.0 (21)	13.19	5.97
1991–1994	4.30	265.1 (23)	11.88	4.48
1995–1998	4.21	376.0 (25)	10.90	2.90
1999–2002	3.50	265.2 (31)	15.87	5.98
Southeastern Sakhalin				
1971–1974	4.09	206.9 (54)	14.54	7.03
1975–1978	5.30	346.1 (50)	16.65	4.81
1979–1982	4.47	605.1 (32)	7.53	1.25
1983–1986	3.81	358.9 (34)	9.42	2.62
1987–1990	4.79	405.2 (26)	27.83	6.87
1991–1994	5.71	374.7 (26)	19.50	5.20
1995–1998	4.06	357.6 (27)	21.50	6.01
1999–2002	3.03	294.1 (27)	14.91	5.07
Iturup Island				
1967–1970	1.04	258.3 (36)	9.07	3.51
1971–1974	1.10	393.5 (30)	13.07	3.32
1975–1978	1.61	349.8 (50)	14.78	4.22
1979–1982	1.52	319.5 (60)	10.86	3.40
1983–1986	1.47	354.8 (51)	18.63	5.25
1987–1990	1.58	373.5 (46)	17.34	4.64
1991–1994	1.85	307.5 (35)	17.40	5.66
1995–1998	1.35	344.0 (20)	19.10	5.55
1999–2002	1.41	419.3 (24)	19.04	4.54

*Proportion of hatchery-released pink salmon fry (%) in parentheses.

the fact that the mortality rate of pink salmon is the highest and changes the most during the first months of marine life (Parker 1962; Ricker 1964; Heard 1991; Karpenko 1998), we can attribute the increase in mortality for year-classes with very abundant fry migrants in Aniva Bay and southeastern Sakhalin (Fig. 5) to density-dependent factors. Further, based on other results for Aniva Bay (Shershnev et al. 1982) and the southeastern Sakhalin coast (Shubin et al. 1996; Ivankov et al. 1999), juvenile pink salmon leave the shallow coastal zone relatively quickly after their downstream migration. Early departure of juvenile salmon will increase the relative losses to predators for non-abundant year-classes. Thus, it likely results in a decline in marine survival of such generations. On the contrary, on Iturup Island pink salmon fry migrate to sea after a period of intense growth in the shallow coastal zone where zooplankton are abundant (Yefanov et al. 1990; Kaev and Chupakhin 2002; Kaev 2003). Perhaps, this is why Iturup pink salmon show less variability in year-class survival during the marine period (survival index ranged from 1.78 to 7.94, SD = 1.56) compared to the southeastern Sakhalin fish (survival index ranged from 0.65 to 11.61, SD = 2.60) and Aniva Bay fish (survival index ranged from 0.79 to 8.25, SD = 2.37).

Despite these differences, there appears to be one common pattern for all three regions which is that changes in stock abundance are mainly the result of pink salmon survival during the marine period. Table 3 shows that some periods are characterized by low survival, and others by high survival. In particular, the increase in pink salmon abundance during the 1990s was determined mainly by the increase in year-class survival during the marine period. While fluctuations in abundance are still somewhat determined by changes in reproductive efficiency in rivers, the changes in pink salmon growth in different years depends entirely on the feeding and habitat conditions in the ocean. Researchers often identify an insufficient oceanic food supply for abundant year-classes of Pacific salmon as an a priori reason for delays in fish growth and, as a consequence, later dates of maturation and migration (Kaganovsky 1949; Gritsenko et al. 1983; Welch and Morris 1994; Bigler et al. 1996). That may explain the later spawning migrations and decreases in growth and fecundity in the 1970s on Iturup Island (Yefanov and Chupakhin 1982). However, this may not always be the case (Kaev and Chupakhin 2003).

Because pink salmon are widely distributed in the northwestern Pacific Ocean (Klovatch et al. 2002), one might think that data on the abundance of different stocks inhabiting the same vast areas are required (Fig. 2). However, we used data for only a few individual stocks. We chose this approach based on the strong relationship between fluctuations in the pink salmon catches in each region (correlation coefficients have ranged from 0.72 to 0.88 since 1946) and the total catches on eastern Sakhalin and the southern Kuril islands. This very abundant group of pink salmon, provides for about 70%, on average, of the Russian pink salmon catch
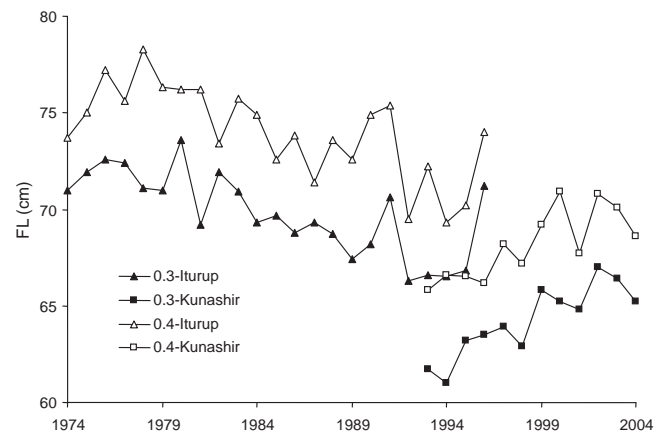
Fig. 6. Changes in fork length in chum salmon ages 0.3 and 0.4 on Iturup and Kunashir islands in 1974–2004. Data collected in 1974–1996 at Iturup Island (Kaev 1999) and since 1993 at Kunashir Island (Kaev and Romasenko 2003).

from the Okhotsk Sea, and is partially isolated during the marine period from the other two large groups—i.e. fish from the rivers in the western and eastern Kamchatka Peninsula. The west Kamchatka and Sakhalin-Kuril juveniles are spatially separated in the Okhotsk Sea until September (Erokhin 2002). This separation is partially maintained during the migration to the Kuril Ridge straits (Temnykh 2004). In other words, the three large groups of pink salmon are already partially separated in the ocean prior to the spawning migration to natal rivers (Temnykh 2004). The possibility of other species (e.g. the comparatively abundant chum salmon) affecting the pink salmon food supply in the Okhotsk Sea and adjacent ocean waters is unlikely because each species has a different diet composition (Fig. 6) (Temnykh 2004).

Density and abundance characteristics of local fish stocks may explain the patterns we are seeing. We note the consistent relationship between changes in escapement timing and fish length, and corresponding changes in pink salmon abundance in all three study areas (Table 2). Changes found in these indices were greater in the Iturup pink salmon than in the southeastern Sakhalin and Aniva Bay fish which can be explained by density-dependent regulation. In order to fully understand the differences in results for the Iturup and Sakhalin fish, we should keep in mind that the data record for the Iturup Island fish is longer. It includes the 1970s, when the concept of the density-dependent regulation was well confirmed.

Peculiarities in pink salmon size composition and escapement timing are also connected with intraspecific structuring. Historically, ichthyologists paid attention to the heterogeneity of the pink salmon migration to the Sakhalin and Kuril rivers (Ivankov 1967, 1986; Gritsenko 1981; Yefanov 1989). Presently, pink salmon from the two ocean groups, one with an early spawning migration and one with later dates, are represented in catches from the study regions (Kaev 2002). Fish from the later group are larger, on aver-

age. The males, especially, increase in length and eventually become larger than females. Based on this information, the increase in catches since the end of 1980s may be the result of the rise in pink salmon abundance, mainly from the later ocean group (Kaev et al. 2004b), which corresponds to the later dates for 50% capture (Fig. 2). However, it appears that since the mid 1990s the migration of the main bulk of pink salmon has tended to shift toward earlier dates. This became even more noticeable at the beginning of the 21st century. Note that the changes in dates of the beginning and the end of the fishing season are not as apparent as the changes in the ratio of early to later-run fish in the catches (Fig. 3).

Finally, one should note the concurrence of the two seemingly different processes. On one hand, the increase in pink salmon abundance and body size, beginning in the second half of the 1980s, coincided in time with a delay in chum salmon growth (Kaev 1994; Helle and Hoffman 1995; Kaeriyama 1996). However, the delay in growth for Asian stocks of chum salmon was observed mainly during their spawning migration in the northeastern Pacific Ocean, while in the Okhotsk Sea and adjacent waters of the Pacific Ocean (the habitat of the pink salmon stocks considered here) such changes in growth of chum salmon were not observed (Kaeriyama 1996; Kaev 1999). On the other hand, the shift toward earlier migration dates coincided in time (second half of the 1990s) with changes in chum salmon growth. We can evaluate this phenomenon by looking at the changes in body length of wild chum salmon populations in the southern Kuril Islands (Fig. 6). At present, there are insufficient data to explain these processes. The patterns observed in both pink and chum salmon, support the point of view of V.P. Shuntov (2000), who reported that since the late 1990s the dynamic processes in the northern Pacific Ocean started to trend in opposite directions. Development of this process may result in a decrease in abundance Asiatic pink salmon stocks.

CONCLUSIONS

The existence in different stocks of permanent and synchronous tendencies toward changes in abundance, as well as in biological indices of fish and escapement timing, points to the important role of long-term cyclical processes in the dynamics of pink salmon stocks in the Sakhalin-Kuril region. At the same time, interannual changes in those indices corresponding with the principles of density regulation have been observed only sporadically, despite the known differences in abundance of pink salmon between odd and even years. Thus, we think that factors connected with habitat changes play the most important role in dynamics of pink salmon stocks.

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Trends in Abundance and Biological Characteristics of Chum Salmon

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Abstract: Chum salmon are the second most abundant salmon in the North Pacific Ocean. In the 1930s, chum salmon were abundant along the Russian coast and in British Columbia. The total catch of chum salmon was small from the late 1940s into the 1970s but increased in the 1980s, reaching historically high levels from the 1990s to the present. Ocean distribution of chum salmon is affected by sea surface temperature. Ocean growth and fish size at maturity decreased in the 1970s and 1980s but recovered in the 1990s and 2000s. These trends in abundance and biological characteristics correlated with ocean conditions. An international cooperative salmon survey by the North Pacific Anadromous Fish Commission may elucidate the mechanisms underlying the relationships among these trends. For conservation and sustainable use of chum salmon stocks, we should monitor the abundance and biological characteristics of chum salmon both in the ocean and in rivers.

Keywords: catch statistics, age at maturity, size at maturity, ocean growth, ocean distribution, chum salmon

INTRODUCTION

The total salmon catches around the North Pacific Ocean were large in the 1930s–early 1940s and the 1980s–2000s (Eggers et al. 2005). These large catches can be attributed in part to the increases in catches of pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon. Chum salmon are the second most abundant salmon (after pink salmon) in the North Pacific Ocean. The geographical range of natal rivers of chum salmon extends from Kyushu Island, Japan, and California in the south, to Siberia and the Arctic coast of North America in the north (Salo 1991). Chum salmon fry migrate to the sea soon after emerging from their freshwater spawning beds in spring. Juveniles migrate offshore in the first summer. Chum salmon grow rapidly in offshore waters in the North Pacific. They can spend 2–7 years in the ocean before returning to their natal rivers for reproduction.

Pacific salmon are one of the dominant zooplankton feeders in the pelagic ecosystem of the subarctic North Pacific and adjacent seas (Shuntov et al. 1999). Long-term changes in some fish populations and in ocean productivity have coincided with the long-term changes in climate (e.g. Beamish 1995). From the 1970s to the 1990s, a decline in the size of mature salmon was observed in populations of many rivers around the North Pacific Rim (see review by Bigler et al. 1996; Helle and Hoffman 1998). Simultaneously, total salmon abundance reached a high level. Some researchers think that the ocean growth of salmon is density-dependent (e.g. Ishida et al. 1993). The abundance of salmon and their prey (i.e. zooplankton and micronekton), and biological characteristics (e.g. body size) should also be affected by climate and ocean conditions.

To examine relationships among trends in chum salmon abundance, biological characteristics, and ocean conditions, we examined time series data from commercial catches, offshore research cruises, and monitoring programs in hatcheries.

MATERIALS AND METHODS

Trends in Abundance

We used catch numbers as an index of abundance based on the assumption that the exploitation rate of chum salmon did not change significantly between years and/or was high enough because long time series of reliable statistics for es-

capement around the North Pacific were not available. The levels of commercial catches were used as an index reflecting the trend in abundance of salmon stocks because the proportion of commercial catch was large in relation to total run size across the entire North Pacific (e.g. Beamish and Bouillon 1993; Klyashtorin and Rukhlov 1998). For specific stocks of Pacific salmon, escapement (or the number of hatchery brood stock in the case of Japanese chum salmon) showed trends similar to those in the commercial catch (e.g. Henderson and Graham 1998; Hiroi 1998). Thus we reasoned that trends in catch may reflect trends in the abundance of chum salmon. Catch statistics for chum salmon were obtained from Eggers et al. (2005).

As another index of chum salmon abundance, we used catch per unit effort (CPUE) calculated from Japanese monitoring surveys in the high-seas areas of the central North Pacific (CNP) and Bering Sea (BS) between 170°E and 170°W in June and July. Japanese fisheries research institutes have monitored salmon abundance and distribution beginning in 1952 using drift gillnets. After 1972, they changed to standard research gillnets consisting of ten different mesh sizes each (Takagi 1975). CPUE was calculated as the number of fish caught per 30 tans of research gillnet (i.e. three tans of each mesh size (one tan is 50 m in length)). Because the maximum number of fish examined was 60 per mesh size per operation, we weighted the age composition by the number of fish in three tans of gillnet by each mesh size in the calculation of CPUE by age group. CPUE was averaged for each research station in waters ranging 5–10°C in sea surface temperature (SST) because chum salmon are most commonly found at temperatures between 5 and 10°C (Nagasawa et al. 2005).

Trends in Ocean Distribution

To evaluate the correlation between chum salmon distribution and sea surface temperature, we examined latitudinal (i.e. south-to-north) distribution of chum salmon in July in the CNP and BS. To estimate latitudinal distribution, we used the ratio of average CPUE of the BS to the sum of averaged CPUEs in the BS and CNP. We averaged CPUE in the high-seas area of the BS and CNP. For CPUE in the CNP, we used data collected north of 45°N.

Trends in Fish Size and Age

For fish size and growth during ocean life, we used measurements of fork length in June and July in Japanese gillnet surveys in the CNP and the BS. We averaged fork length of chum salmon caught using a research gillnet by age group. Although a single-mesh gillnet usually has a strong size-selectivity, research gillnets consisting of ten different mesh sizes are less size-selective (Takagi 1975). Ocean growth was calculated as the difference between average fork length of an age group in a year and the average fork length of the

same year-class one year before:

$$G_{a,y} = FL_{a,y} - FL_{a-1, y-1}$$

where $G_{a,y}$ is ocean growth of age group a at year y, and $FL_{a,y}$ is average fork length of age group a at year y.

For trends in size and age of mature chum salmon, we used fish measurement data from the monitoring of hatchery brood stocks in the Ishikari River, Hokkaido, Japan. We considered the Ishikari River chum salmon as representative of Asian chum salmon stocks because trends in size and age of mature fish were similar to other Asian stocks (Ishida et al. 1993). We averaged the fork length of four-year-old fish because the dominant age of maturation was four years old in the river. Age at maturity by brood year was weighted by the numbers of adults caught in the river and averaged.

Relationships among Trends

For the relationships among ocean conditions, abundance, and biological characteristics of chum salmon, we used the multiple regression analysis with a stepwise selection of independent variables ($P \leq 0.05$ to add, $P \geq 0.10$ to remove). As indices of ocean conditions, we used the average Pacific Decadal Oscillation (PDO) index from June to September and average SST at 47–49°N, 179°E–179°W for July (SST, CNP) obtained from the Japan Meteorological Agency. PDO was the leading principle component from the empirical orthogonal function analysis of monthly sea surface temperature anomalies poleward of 20°N in the Pacific basin, which was consistent with salmon catches in the northeast Pacific (Mantua et al. 1997). As an index of spawner abundance, we used the time series data of chum salmon catches in Russia and Japan (excluding offshore catches) because Asian stocks were dominant in the CNP and the BS (Seeb et al. 2004). Coastal catches should be proportional to the level of escapement under the assumption that the exploitation rate did not change significantly between years and/or was high enough. Catches and CPUEs were log-transformed as usually recommended for abundance statistics.

RESULTS

Trends in Abundance

There are two periods with large catches of chum salmon around the North Pacific Ocean: the 1930s and early 1940s, and the 1980s to 2000s (Fig. 1). In the 1930s and early 1940s, large catches of chum salmon were recorded in Russia, but catches in Japan were relatively small. In the same period, catches in British Columbia and southeast Alaska were large in comparison to other areas in North America. After World War II, Japanese high-seas fisheries grew under the conventions of two treaties: the International Convention for the High Seas Fisheries of the North Pacific
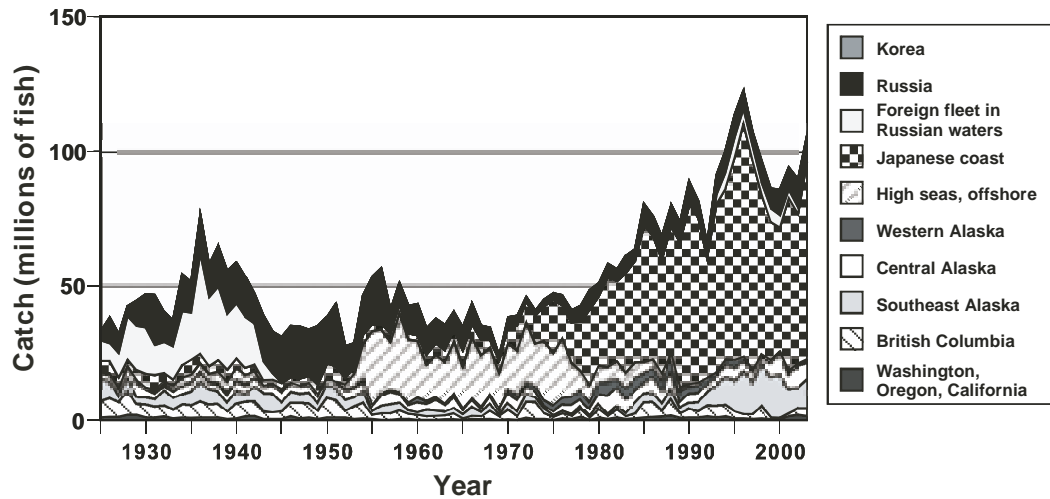
Fig. 1. Catches of chum salmon by area around the North Pacific Ocean, 1925-2003 (modified from Eggers et al. 2005). The Korean catch could not be distinguished from catches in other regions because of the small numbers.
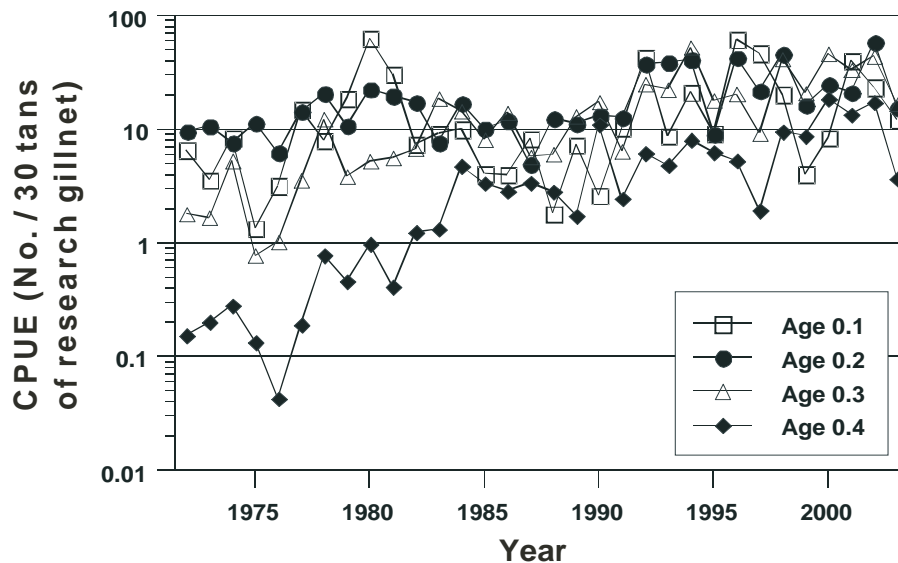
Fig. 2. Catch per unit effort (CPUE, number of fish per 30 tans of research gillnet) of chum salmon by age in waters 5–10°C in sea surface temperature in the central North Pacific Ocean and the Bering Sea, 1972-2003.

Ocean involving Japan, Canada and the United States, and the USSR – Japan Fisheries Agreement. During the same period, catches in coastal and river fisheries were small both in Asia and North America. During the latter half of the 1970s and 1980s, catches in the high-seas areas gradually decreased due to reduced quotas, and limits in fishing areas and fishing durations for high-seas fisheries. Simultaneously, the total catch of chum salmon increased significantly, largely due to the contribution from Japanese coastal fisheries. In 1993, high-seas salmon fisheries were closed due to the Convention for the Conservation of Anadromous Stocks in the North Pacific Ocean and the United Nation's General Assembly resolution 46/215, which ensured a moratorium on large-scale pelagic high-seas driftnet fishing. Since the

1980s, chum salmon catches along the Japanese coast have increased significantly, but catches in Russian waters have remained small. In North America, catches in southeast Alaska have increased, but catches in other areas have remained small. At the present time, chum salmon catches and abundance are at historic high levels.

Chum salmon CPUEs in the high-seas areas of the CNP and BS have increased since the 1970s (Fig. 2). Although the CPUE of age 0.1 fish fluctuated around 10 ($r = 0.281$, $P = 0.119$), CPUEs of age 0.2, 0.3, and 0.4 fish increased ($r = 0.556$, $P < 0.001$ for age 0.2; $r = 0.741$, $P < 0.001$ for age 0.3; $r = 0.762$, $P < 0.001$ for age 0.4). This increase in CPUE coincided with the increase of overall coastal catches around the North Pacific ($r = 0.474$, $P = 0.006$ for age 0.2 CPUE; $r =$
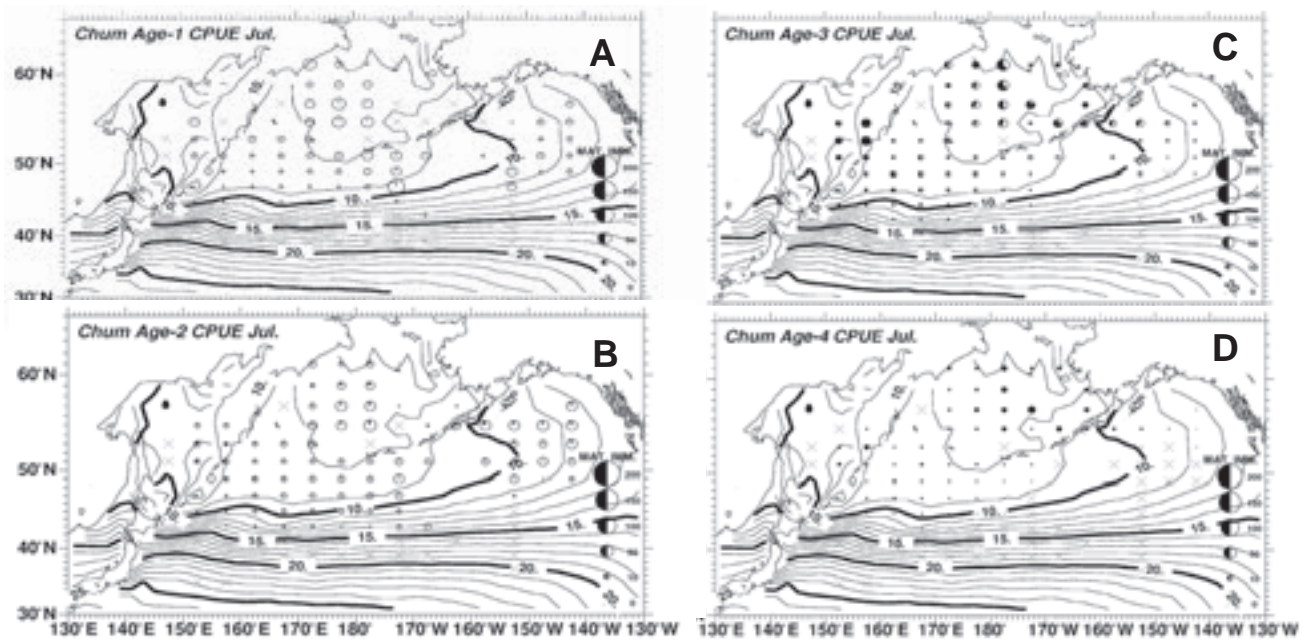
Fig. 3. Ocean distribution of chum salmon in the North Pacific Ocean for age 0.1 fish (A), age 0.2 fish (B), age 0.3 fish (C), and age 0.4 fish (D) in July in 1972–2002. Size of circle indicates catch per unit effort (CPUE, number of fish per 30 tans of research gillnet). Solid areas in circles indicate the proportion of maturing fish; MAT maturing, IMM, immature. "X" indicates zero CPUE. Lines indicate sea surface temperature (°C).
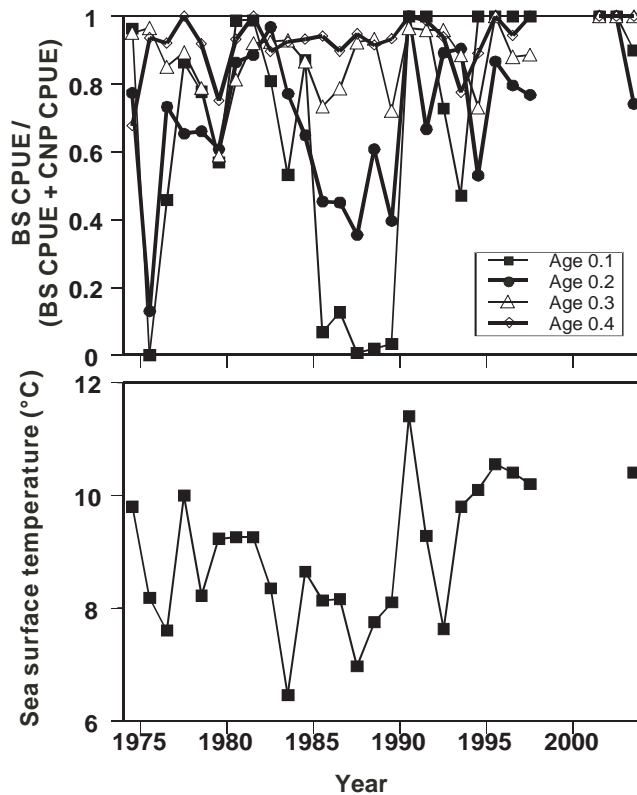
Fig. 4. Ratio of catch per unit effort (CPUE, number of fish per 30 tans of research gillnet) of chum salmon in the Bering Sea (BS) to the sum of CPUEs in the central North Pacific (CNP) and BS by age group with mean sea surface temperature (SST) at 47–49°N, 179°E–179°W July, 1974–1997, 2001–2003.
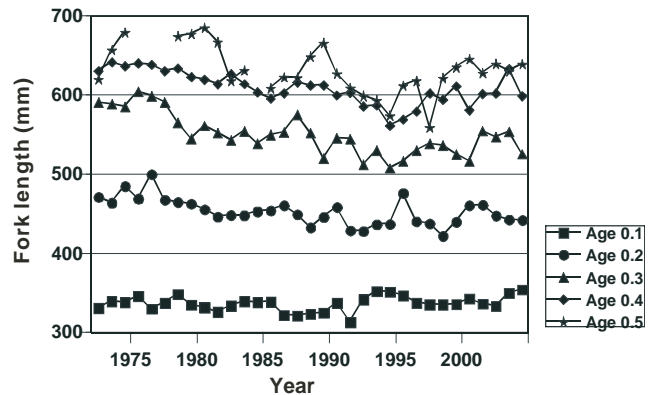
Fig. 5. Mean fork length of chum salmon caught in research gill-nets in the central North Pacific and the Bering Sea by age group, 1972–2004.

0.607, $P < 0.001$ for age 0.3 CPUE; $r = 0.592$, $P < 0.001$ for age 0.4 CPUE).

Ocean Distribution

In July, chum salmon were distributed mainly in the BS and the Gulf of Alaska (Fig. 3). Age 0.1 fish were distributed in waters with SST < 10°C in the CNP as well as the BS (Fig. 3A). The distribution of age 0.2 fish was similar to the distribution of age 0.1 fish (Fig. 3B). On the other hand, 0.3 and 0.4 fish were distributed mainly in the BS (Fig. 3C, D).

Age 0.1 and 0.2 fish were distributed in the BS when SST were high in the CNP (Fig. 4). At low SST, these fish
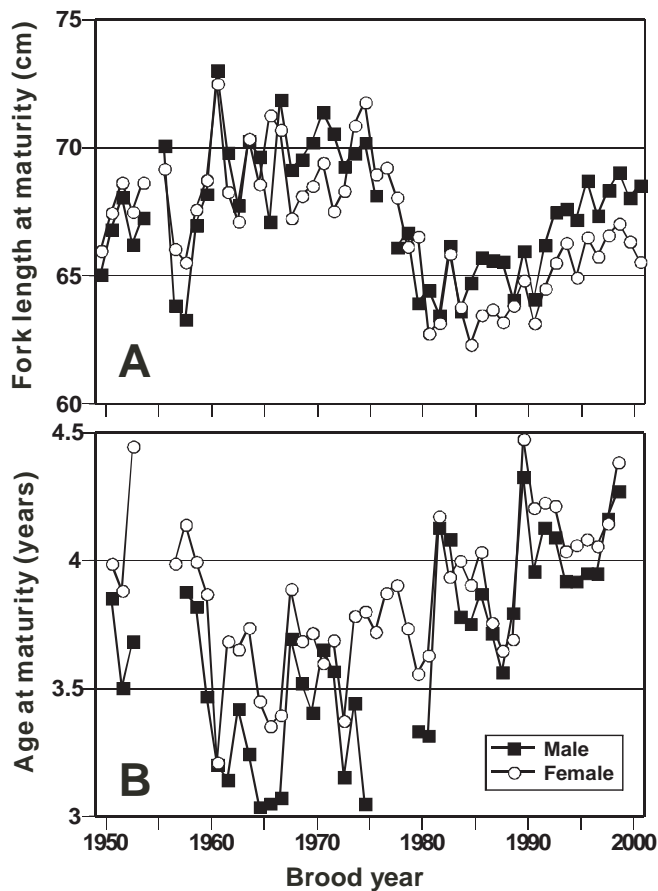
Fig. 6. Mean fork length of mature four-year-old chum salmon (A) and mean age of mature chum salmon by brood year (B) in the Ishikari River, Hokkaido, Japan.

were also distributed in the CNP. The ratios of age 0.1 and 0.2 fish distributed in the BS correlated positively with SST in the CNP ($r = 0.684$, $P < 0.001$ for age 0.1 and $r = 0.421$, $P = 0.036$ for age 0.2). On the other hand, age 0.3 and 0.4 fish were always distributed in the BS. The ratio of 0.3 and 0.4 fish distributed in the BS did not correlate with SST in the CNP ($r = 0.129$, $P = 0.536$ for age 0.3, and $r = 0.083$, $P = 0.695$ for age 0.4).

Trends in Fish Size and Age

Mean fork length by age group of chum salmon decreased from the 1970s to the 1990s, but has increased recently (Fig. 5). While mean fork length of age 0.1 fish did not change appreciably ($r = 0.229$, $P = 0.200$), mean fork lengths of age 0.2, 0.3, 0.4, and 0.5 fish decreased from the 1970s to the mid 1990s ($r = -0.575$, $P < 0.001$ for age 0.2; $r = -0.717$, $P < 0.001$ for age 0.3; $r = -0.672$, $P < 0.001$ for age 0.4; $r = -0.448$, $P = 0.015$ for age 0.5). Since 1994, fork lengths of age 0.3, 0.4, and 0.5 fish have increased. The larger change in fork length of fish older than age 0.1 fish indicate that ocean growth in offshore waters changed tem-

porally. Ocean growth of chum salmon has recovered since the 1990s.

Mean fork length of mature four-year-old chum salmon was large in the 1960s and 1970s year-classes, decreased in the 1970s and 1980s ($r = -0.846$, $P < 0.001$ for males and $r = -0.747$, $P < 0.001$ for females in the 1971–1990 year-classes), and recovered in the 1990s and 2000s ($r = 0.845$, $P < 0.001$ for males and $r = 0.802$, $P < 0.001$ for females in the 1991–2004 year-classes) (Fig. 6A). These changes coincided with changes in fish size during ocean life ($r = 0.543$, $P = 0.001$ for males and $r = 0.595$, $P < 0.001$ for females with ocean fork length of age 0.3 fish).

The mean age of mature fish decreased in the 1950s year-classes but has increased since the 1960s ($r = 0.813$, $P < 0.001$ for males and $r = 0.745$, $P < 0.001$ for females after the 1960 year-class) (Fig. 6B).

Relationships among Trends

The regression analysis showed a synchronization of trends in ocean conditions, abundance, and biological characteristics of chum salmon (Fig. 7). Offshore CPUE of age 0.2 fish correlated with the coastal catches in Asia three years before. Coastal catches should be proportional to spawner abundance, if the exploitation rate did not change significantly and/or was high enough. CPUE correlated also with the summer PDO two years before, which should correlate with ocean conditions during the first summer of ocean life. CPUE of age 0.2 fish correlated with CPUE of age 0.3 fish of the same year-class and with coastal catches one year after, which included mainly age 0.3 (four-year-old) fish.

Ocean growth of age 0.2 fish correlated negatively with CPUE (Fig. 7). Fork length of age 0.2 fish in offshore waters correlated positively with age at maturity for the same year-class and size of mature fish in the same year. These relationships indicate that trends in abundance and biological characteristics are affected by ocean conditions.

Sea surface temperatures in the CNP in July correlated positively with the ratio of the BS CPUE (Figs. 4 and 7). This indicates that ocean distributions of chum salmon are affected by SST.

DISCUSSION

Abundance and Ocean Conditions

Regions in which large catches of chum salmon were recorded were different in the 1930s–early 1940s compared to the 1980s–2000s. While large catches were recorded in Russia, southeast Alaska, and Canada in the 1930s and early 1940s, large catches recorded in the 1980s–2000s were in Japan and southeast Alaska where hatchery programs have been well developed. This supports the hypothesis that the recent increases in chum abundance may be a result of the development of hatchery programs and improved hatchery
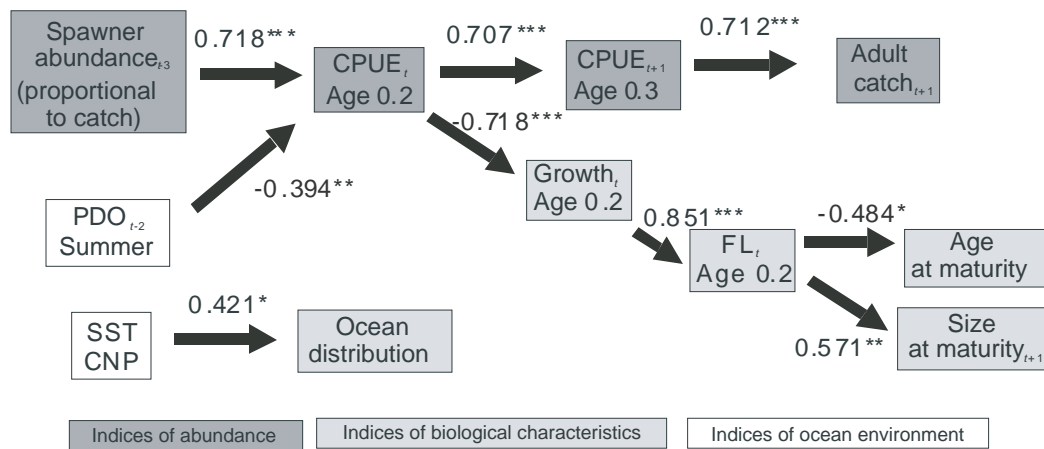
Fig. 7. Relationships among trends in ocean conditions, abundance, and biological characteristics of chum salmon in year *t*. PDO, Pacific Decadal Oscillation; SST, sea surface temperature; CNP, central North Pacific; FL, fork length. Numeral indicates a standard partial regression coefficient or correlation coefficient and asterisks indicate statistical significance (t-test, *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$).

techniques (Mayama 1985; Kaeriyama 1998). However, in a recent review of hatchery programs in Hokkaido, Japan, Morita et al. (2006) indicated that climate change, the closing of high-seas fisheries, and improvements in water quality, as well as hatchery programs, could explain the increase in salmon abundance. To attribute the effectiveness of hatchery programs to the recent increases in chum salmon abundance, we need more information on topics such as differences in ocean mortality of hatchery and wild fish, reliable escapement estimates, and freshwater mortality of wild fish.

An alternative hypothesis to explain the different dynamics of chum salmon stocks among regions is the effect of climate change on local populations. Large-scale climate change strongly affects salmon population dynamics (e.g. Beamish and Bouillon 1993; Mantua et al. 1997). Large-scale climate change has resulted in different responses among local ocean micro-climates and ecosystems (Mantua et al. 1997; Nagasawa 2000). Salmon survival responded differently to local SST in northern and southern areas of the Pacific coast of North America (Mueter et al. 2002). Inverse salmon production regimes were observed between Alaska and the west coast of the United States (Hare et al. 1999). Large-scale climate change can result in varying patterns in local population dynamics of chum salmon.

We found correlations between mean summer PDO, adult catches in Asian coastal areas, and offshore CPUEs of chum salmon. The relationship between the ocean climate (e.g. PDO or Aleutian Low Pressure Index) and salmon abundance has been reported by many authors (e.g. Beamish and Bouillon 1993; Mantua et al. 1997). However, the mechanisms underlying the relationship(s) between large-scale climate indices and salmon abundance have not yet been well clarified. Large-scale climate indices often outperform local climatic factors in predicting ecological processes of a local population, when measures of local climate parameters used by ecologists fail to capture complex associations between

climate conditions and ecological factors (Hallet et al. 2004). The strong relationship between local ocean conditions (e.g. coastal sea surface temperature or upwelling) and salmon abundance has also been reported (Fukuwaka and Suzuki 2000; Mueter et al. 2002). Asian chum salmon dominated in the CNP and the BS when we used CPUE as an abundance index in offshore waters (Neave et al. 1976; Seeb et al. 2004). Temporal patterns in population dynamics were not synchronous among chum stocks in Asia (Salo 1991). Different temporal patterns in local population dynamics could be due to differences in terrestrial or ocean environments, or mechanisms controlling population abundance. Although local ocean conditions (or climate) and spawner abundance of chum salmon may determine the abundance of a local population, a large-scale climate index (i.e. PDO) may correlate with offshore CPUE, which includes many local populations.

Distribution and Ocean Conditions

We showed that the offshore distribution of age 0.1 and 0.2 chum salmon was different from that of 0.3 and 0.4 fish and changed with SST in July. It is well known that the offshore distribution of Pacific salmon is affected by SST. Manzer et al. (1965) reviewed the offshore distribution of gillnet catches in the Japanese salmon fishery and the International North Pacific Fisheries Commission salmon research. They indicated that geographical and SST ranges of salmon distribution changed with season. Neave et al. (1976) showed that immature chum salmon were distributed in waters warmer than those occupied by maturing fish from April to June. Sea surface temperature may influence growth and feeding activity because chum salmon are distributed in the surface layer. Pacific salmon might select an SST range to either maximize or ensure somatic growth (Welch et al. 1995; Rand 2002). Maturing chum salmon begin their homing migration

in June (Neave et al. 1976). While younger chum salmon may actively select waters with a preferred range of SST to maximize somatic growth, older and maturing fish might be distributed in cooler waters of the BS and less affected by SST.

Abundance, Ocean Growth, Age, and Size at Maturity

We found a negative correlation between offshore CPUE and ocean growth of chum salmon. Ishida et al. (1993) showed a negative correlation between CPUE and fish size using Japanese research data in offshore CNP, and discussed density-dependent growth of chum salmon. Some authors thought that the density-dependent growth of Pacific salmon could be the result of competition for food (e.g. Ishida et al. 1993; Bigler et al. 1996). Peterman (1987) showed that intraspecific competition for food, such as the negative correlation between fish size of Fraser River pink salmon and the number of fish per zooplankton biomass at ocean station P in the Gulf of Alaska. In addition, interspecific competition for food (i.e. zooplankton) may occur among salmon species or other zooplankton feeders (e.g. Ruggerone et al. 2003). To clarify the mechanisms of density-dependent growth of Pacific salmon, it is necessary to study competition within and among species of salmon and other plankton feeders in the ecosystem of the North Pacific and the BS.

Ocean growth affected age at maturity of the same year-class of chum salmon. Fish size was strongly related to individual fitness because large females can produce large numbers of eggs and large males have some advantages in mating competition (Hendry et al. 2004). Parr of Atlantic salmon males exceeding a threshold size initiated maturation (Myers et al. 1986; Baum et al. 2004). However, physiological studies indicate that somatic growth is linked closely with sexual maturation mediated by the endocrine system, such as the secretion of growth hormone and insulin-like growth factor-I in vertebrates (reviewed by Chandrashekar et al. 2004). Growth history affected maturation stronger than fish size in chum salmon (Morita and Fukuwaka 2006). Although a threshold size for maturation may be necessary to reach sexual maturity, a proximate factor initiating sexual maturity may be the level of ocean growth in chum salmon.

Fork length of age 0.2 fish correlated negatively with age at maturity and positively with size at maturity. Several authors have reported that a decrease in size and an increase in age of mature salmon occurred simultaneously in many populations around the North Pacific from the 1970s to the 1990s (e.g. Ishida et al. 1993; Bigler et al. 1996). In the theory of life-history strategy, an optimal response to a reduced growth rate is an increase in age and decrease in size at maturity (Stearns 1992). Using the scale back-calculation techniques, Morita et al. (2005) indicated that a recent increase in age and decrease in size of Japanese chum salmon could result from a growth reduction during ocean life, supporting the hypothesis that change in age and size at maturity

is an adaptive response.

International Survey for Mechanisms

The North Pacific Anadromous Fish Commission conducted an international survey from 2002 to 2006 called the Bering-Aleutian Salmon International Survey (BASIS) that will form the foundation for long-term, large-scale ecosystem research on salmon in the Bering Sea (NPAFC 2001). The goal of BASIS is to understand the mechanisms underlying the effects of environmental variation and density-dependence on the salmon carrying capacity in the Bering Sea. Key factors determining chum salmon production may occur in the Bering Sea as well as in coastal waters during early ocean life because ocean growth of chum salmon is higher in summer than in other seasons (Ishida et al. 1998). BASIS may elucidate the mechanisms underlying the relationship between trends in abundance and biological characteristics of chum salmon.

CONCLUSIONS

At present, the size and age of chum salmon continues to increase even though chum salmon abundance around the North Pacific is at the highest level ever. In the past, abundance and biological characteristics of chum salmon fluctuated on a decadal scale. Abundance and biological characteristics correlated with each other and were affected by ocean or climate conditions. For conservation and sustainable use of chum salmon stocks, we should monitor the abundance and biological characteristics in rivers and the ocean.

ACKNOWLEDGEMENTS

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Trends in Abundance and Feeding of Chum Salmon in the Western Bering Sea

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Abstract: Results from surveys of the western Bering Sea and adjacent Pacific epipelagic waters, performed by TINRO-Centre are reported. Surveys of the nekton community were conducted from 1986 through 2005, annually. Information on the distribution of all chum salmon by age group, the abundance and biomass of chum salmon, and other fish in the western Bering Sea and adjacent Pacific Ocean water are reported. Chum salmon diet differed according to location in the western Bering Sea.

Keywords: chum salmon, catches, biomass, abundance, zooplankton, consumption

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) have been studied for more than 100 years and yet considerable interest in this genus of fish remains. Despite significant progress in our knowledge of Pacific salmon biology, there are still many issues relating to the reliability of short-term and long-term forecasts of fish abundance and population dynamics. With the development of marine studies of the Pacific salmon in the 1950s, new information about the sea life of these fish appeared, expanding our knowledge about ocean distribution of salmon, salmon feeding behavior, mortality, and factors influencing abundance (Takagi et al 1981; Heard 1991; Salo 1991; Myers et al. 1996; Shuntov et al. 1996).

Beginning in the mid-1980s, studies of Pacific salmon ocean life history have been conducted and large amounts of data collected and tabulated in databases. These data include information pertaining to hydrology, nekton, and zooplankton. Twenty years of research into the Far East seas substantially increased the existing knowledge about salmon ecology during foraging and spawning migrations and facilitated the collection of new data on feeding behavior and trophic relationships in marine ecosystems. This paper presents data collected during TINRO-Centre investigations in the Far Eastern seas from the mid-1980s through 2005. The role of chum salmon (*O. keta*) in the Bering Sea ecosystem, the current state of chum salmon stocks and trends in their abundance are also analyzed.

MATERIALS AND METHODS

Chum salmon and other pelagic nekton were collected in a standard midwater rope trawl type 80/396 m for surveys conducted during 1986 to 1995, and in a standard midwater rope trawl type 108/528 m for surveys conducted during 2002 to 2005. The length of the headrope was 80 m for the 80/396 and 108 m for the 108/528, and the perimeter of the trawl opening was 396 m or 528 m, respectively. Rigging specifics are described by Volvenko (2000). Trawl operations lasted 24 hours. The trawl hydrodynamic plate was maintained at 0 m (the position of the plate was verified by acoustic readings and by sight) and the length of the warp was 245–280 m. Each trawl was towed for one hour.

The abundance (in millions of individuals) and the biomass (in thousands of tons) of chum salmon, other fishes and cephalopods were calculated by multiplying the average density (individuals/km^2) and mass (kg/km^2) for the particular species times the area of the biostatistical region. Oceanographic conditions were sampled at the same approximate location of the trawl tows. A "Neil Brown" MARK-II CTD was used to measure temperature and salinity to a maximum depth of 1,000 m.

To sample plankton, a Juday net (mouth opening – 0.1 m^2, kapron mesh #49, mesh size - 0.168 mm) was used during both day and night. Plankton was sampled at every station at the approximate location of the trawl tows. The plankton net was towed in 200-0 m strata in deepwater areas or between bottom and 0 m in shallow areas. Each plankton sample was divided into 3 fractions: small (< 1.5 mm), medium (1.5 to 3.5 mm), and large (3.5 mm or more). The biomass was determined using a volumeter. When calculating plankton biomass, the correction factors were as follows: for the small fraction -1.5; for the medium fraction - 2.0; for the large fraction: euphausiids and chaetognaths shorter than 10 mm - 2.0; for specimens 10 to 20 mm long - 5.0; for specimens over 20 mm in length - 10.0. The correction factor for hyperiids

shorter than 5 mm - 1.5; 5 – 10 mm long - 5.0; for copepods under 5 mm - 2.0; over 5 mm - 3.0.

Chum salmon feeding patterns were examined in groups according to body size: 10–20 cm, 21–30 cm, 31–40 cm, 41–50 cm, 51–60 cm, and > 61 cm. The samples including from 10 to 25 stomachs of the same body size group were selected from catches and processed without prior fixation. Upon weighting the sample the species composition of food, the percentage of most numerous species and other typical parameters were analyzed. The stage of food digestion was evaluated using 5-step scale. The index of stomach fullness was calculated as the relation of food mass in the stomach divided by fish body weight times 10,000. The daily food intake was calculated with due regard to feeding peaks. Thus, the daily food intake was counted as the overall sum of all prey consumed for every period of time studied.

RESULTS AND DISCUSSION

In the last 50 years, the Bering Sea has been warmer than normal. In general, the 1990s appeared relatively warm, and winters were without extensive ice cover. However, a shift towards cooling occurred in the atmosphere and hydrosphere in the North Pacific in 1998, which led to an increase in the extent of ice in the Bering Sea during winter (Ustinova et al. 2004).

The cold regime persisted in 2001–2002, and though positive temperature anomalies occasionally dominated in certain areas, subarctic currents were rather strong. During four years from 2002 to 2005, areas with the highest sea surface temperatures were distributed in the southwestern Bering Sea (Khen and Basyuk 2004). The year 2003 was anomalously warm. In late June 2005, the sea surface temperature was close to the long-term average over almost in the entire western Bering Sea, and positive anomalies of sea surface temperature were observed in northern areas. Increasing trends of the hydrothermal regime in the Bering Sea appeared as a result of shifts in atmospheric processes. In particular, in 2003 and 2004, trajectories of summer and winter centers of atmospheric activities (Far Eastern and Aleutian depressions) were displaced somewhat farther south than in cold seasons (Glebova in press).

Beginning in the late 1990s, water exchange rate between the Pacific Ocean and the Bering Sea showed an increasing trend (Table 1). The amount of water flowing through Kamchatka Strait may serve as an indicator of trends in annual variability of water exchange rate between the ocean and the sea. Most of the water flowing out of the sea is discharged through this strait, while the inflow of oceanic waters occurs mainly through other Aleutian passes. Intensification of oceanic water inflow has been registered in the summers of 2003 and 2005, and was the highest over the last 7 years in 2005. In the 2000s, patterns of geostrophic circulation were close to the known patterns of currents. Speeds of major geostrophic currents were also the highest at that time (Khen

Table 1. Average water flow in the 0-1500 m layer of Kamchatka Strait in summer and autumn by year.

Year	Water flow (10^8 m^3/s)
1999	3.37
2000	1.65
2001	5.18
2002	5.35
2003	6.05
2004	4.81
2005	6.60

and Basyuk 2004).

The above-mentioned observations suggest that in the last 10 years, the warm period of the mid-1990s was succeeded by a short-term cold period at the beginning of the 20th and 21st centuries in the Bering Sea, and the last years (early 2000s) again appeared rather warm. We may expect that these shifts from warm to cold regimes and back will persist in future.

The structure of nektonic communities also experienced notable rearrangements in the last 20 years in the Bering Sea. Walleye pollock (*Theragra chalcogramma*) was a predominant species in epipelagic nekton in many Bering Sea areas in the 1980s (Fig. 1). The stock collapsed in the 1990s, which was associated with natural decrease in the species' reproductive rate. Walleye pollock almost disappeared from offshore areas, but retained its position as a dominant species in the northern shelf and upper slope areas. At the same time, Pacific salmon, Pacific herring, mesopelagic fish and occasionally atka mackerel have increased their abundances in deepwater offshore areas.

Beginning in the late 1980s (1986–1990) and early 1990s (1991–1995) and up to the 2000s (1998–2004), the number of chum salmon per square kilometer has increased considerably in the western Bering Sea. Estimates of relative abundance of chum salmon averaged 29, 50 and 543 individuals per square kilometer during these periods, respectively. The total relative abundance of chum salmon was assessed at 4785, 4677 and 60,785 individuals per square kilometer in these years, respectively.

Summer surveys in 2003 and 2005 revealed that in the western Bering Sea, the combined biomass of all Pacific salmon has increased three times compared to values in the late 1980s and early 1990s. Salmon biomass accounted for 78 and 85% of total fish biomass, or 842.2 and 464.2 thousand tons in the upper epipelagic zone in 2003 and 2005, respectively. Chum salmon accounted for 63 and 54% of total fish biomass in 2003 and 2005, respectively.

Data obtained during large-scale autumn surveys across the entire western Bering Sea appeared consistent with these data as Pacific salmon dominated epipelagic nektonic communities in the Bering Sea (Fig. 2). The proportion of
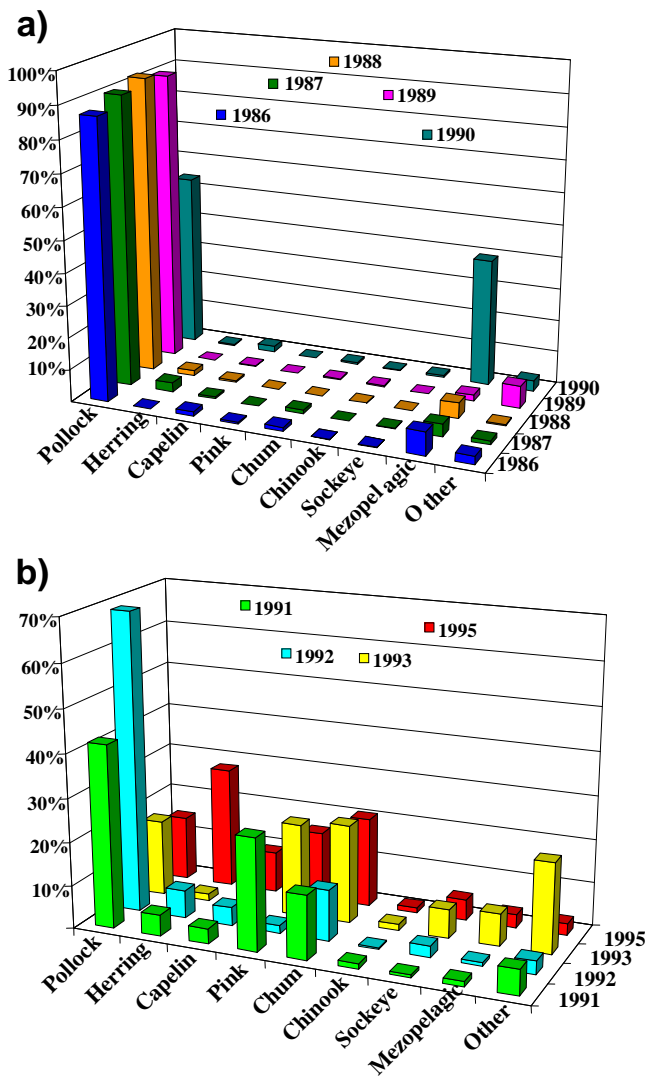
Fig. 1. Fish biomass (%) in the southwestern deepwater Bering Sea in the late 1980s (a) and early 1990s (b).

Fig. 2. Biomass (%) of Pacific salmon and other fish in the upper epipelagic layer in the western Bering Sea during autumn 2002 (a), 2003 (b) and 2004 (c).

salmon in the total fish biomass appeared to be low only in several cases. First, the proportion was low when lantern fishes increased in abundance in the upper layers (these fish migrate from deep to surface layers only at night) in 2002. Second, salmon were relatively less abundant in areas where juvenile walleye pollock occurred in large quantities, e.g., in the Navarin-Anadyr region in 2003 while juvenile pollock accounted for 98% of the total species biomass, which was assessed at 710 thousand tons in that area. Chum salmon appeared the most abundant Pacific salmon species, and accounted for 15.4–39.2% of total fish biomass which amounts from 2,180.9 (2002) to 1,424.1 (2003) to 371.8 (2004) thousand tons.

It is worth noting that immature chum salmon accounted for the bulk of the total chum salmon biomass in the western Bering Sea upper epipelagic zone during summer and autumn in the 2000s. Maturing chum salmon aggregate in

coastal areas in summer, and those maturing fish that are going to spawn outside the western Bering Sea area, start their ocean-ward migrations, and by autumn, most of them are found in the Pacific Ocean. At the same time, in autumn, chum salmon juveniles migrate offshore from coastal areas.

During BASIS research, the highest biomass of immaturing chum salmon, almost 594.45 thousand tons, was found in the western Bering Sea in summer 2003. Extremely high abundance of chum salmon in the western Bering Sea in summer 2003 was presumably associated with an intensive flow of water from the east to the western part of the sea, and with favorable forage conditions in the latter area. In summer 2005, the biomass of foraging chum salmon was estimated

Table 2. Biomass (in thousands of tons) of chum salmon in the upper epipelagic layer in the western Bering Sea from 2002 to 2005.

Group	Autumn 2002	Summer 2003	Autumn 2003	Autumn 2004	Summer 2005
Juvenile	2.21	0.01	3.07	1.63	-
Immature	316.83	594.45	246.28	132.76	144.9
Maturing	15.94	90.01	10.82	11.32	149.05
Total	334.98	684.47	260.17	145.71	293.95

at 144.9 thousand tons, which was four times lower than in 2003. No summer data were available from the western Bering Sea in 2002 and 2004. The abundance and biomass of chum salmon showed a positive long-term trend (from the 1980s to the 2000s); however, these parameters fluctuated from year to year. Autumn biomass of immature chum salmon varied from 132.76 thousand tons in 2004 to 316.83 thousand tons in 2002 in the western Bering Sea (Table 2).

The autumn abundance of all age groups of immature chum salmon decreased in the 2000s. For example, mean catch per unit effort (CPUE) for age 0.1 chum salmon decreased from 28.9 individuals per hour trawling (IPHT) in 2002 to 17.8 IPHT in 2003 and 8.2 IPHT in 2004. CPUE for 0.2 age chum salmon decreased, from 5.96 to 4.39 and 1.85 IPHT, while that for older fish decreased from 2.55 to 1.04 and 0.57 IPHT for the same years.

Distribution patterns of immature chum salmon were similar in years of high and low species abundance in the western Bering Sea. In 2002–2004, the highest density of immature chum salmon was observed in the deep area of the Commander Basin, while to the north and south of these areas, catches were much lower. Individuals in the second year of marine life dominated the catches of immature salmon in the Bering Sea in autumn. Figure 3 shows that maximum catches of this age group were also distributed mainly over the deep Commander Basin. Older chum salmon leave the Bering Sea earlier and would not be expected to be numerous in the catches at this time. These older chum salmon in their third year of marine life are distributed mainly near the Commander Islands and east of the Commander Basin. Mean body lengths of chum salmon were distributed as follows: most chum salmon from 35 to 44 cm in length occupied deep basins of the western Bering Sea during autumn, and larger fish (age 0.2 and older) were more numerous in northern areas and in waters adjacent to the Commander Islands, particularly, in the ocean (Fig. 3).

Based on the distribution patterns of immature chum salmon, the deepwater Commander Basin could be considered as an optimal foraging area for fish in the second and third years of marine life. Large catches of chum salmon are distributed over wider areas when abundance is increasing.

A significant positive correlation between normalized catches for immature two- and three-year-old chum salmon is shown in Fig. 4a. Correlations between relative densities of age 0.1 and 0.2 chum salmon and sea surface temperature were not significant (Fig. 4b). Chum salmon tend to live mainly within a temperature range of 6 to 11°C. The strong relationship between catches for two- and three-year old chum salmon may suggest that similar mechanisms govern their distribution; however, temperature does not appear to affect distribution. For example, in autumn 2002, immature chum salmon aggregated mainly in the area with negative seas surface temperature anomalies, while in autumn 2003 and 2004, in the area of positive anomalies.

Forage conditions, in particular, prey availability in forage areas, could be considered as one of the most important factors governing immature chum salmon distribution. Small and medium-sized animals dominate the zooplankton community in most areas of the eastern Bering Sea, while large-sized zooplankton are more abundant in the western Bering Sea and adjacent waters of the Pacific Ocean. Large zooplankton also form a forage base for nektonic animals. Copepods and chaetognaths comprise the bulk of the large zooplankton biomass in most Bering Sea areas. In the western part of Bering Sea euphausiids, amphipods and pteropods (major prey for chum salmon) were more abundant (Volkov et al. 2004).

A negative trend in the biomass of forage zooplankton has been observed during the last three years; however, fluctuations in zooplankton abundance occur at regular intervals of about 5–7 years in the Far Eastern seas of Russia. In 2003, the biomass of large zooplankton was the smallest in the eastern part of the sea, particularly, on the shelf of Bristol Bay, where representatives of this size group comprised about 9% of the total zooplankton biomass. In the deepwater marine areas, the biomass of large zooplankton was much greater, and accounted for 78–85% of the total zooplankton biomass (Volkov et al. 2004). Therefore, western areas of the sea, particularly, the deep basin, are favorable forage areas for Pacific salmon, particularly, for chum salmon.

Chum salmon diet may vary in different regions and from year to year. From the late 1980s to the early 1990s, chum salmon (> 30 cm body length) preyed predominantly on large zooplankton (87–93% of the diet), and less intensively on nektonic fish and squid (7–13% of the diet) in the Commander Basin (Fig. 5). In the 1980s, euphausiids and hyperiids comprised a larger portion of the chum salmon diet. In the 1990s, the chum salmon diet consisted mainly of pteropods, and to a lesser extent euphausiids and hyperiids. Significant annual variability has been observed in the

chum salmon diet. For example, pteropods may serve as the main prey item in some years, and be of minor importance in years of low abundance. The same is true for other groups of planktonic animals, such as euphausiids, copepods and hyperiids. The observed shifts in the feeding activity of chum salmon are not always associated with annual changes

in the stock abundance of major large zooplankton groups. Availability and abundance of small nektonic animals, which occasionally dominate in the diet of chum salmon of older age classes, may account for the observed variability in the fish diet.

In 2002 and 2003, chum salmon preferred to prey upon
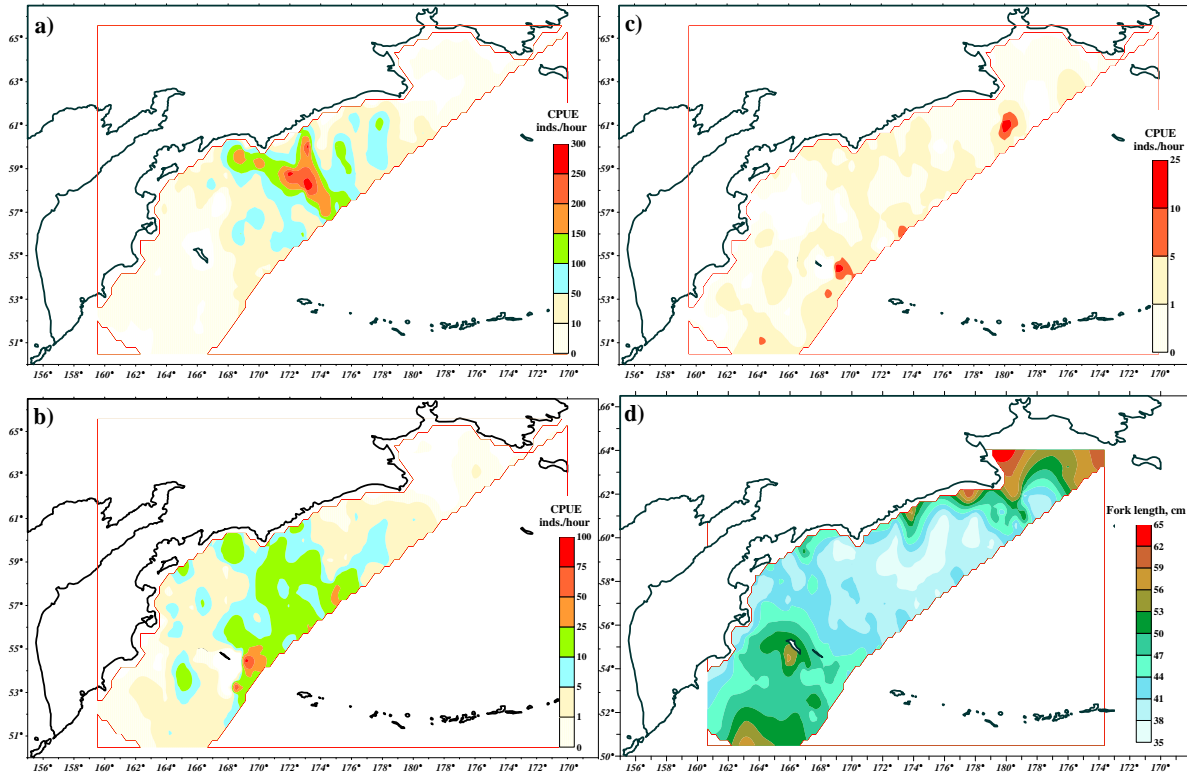
Fig. 3. Average CPUE (individuals per 1-h trawling) distribution of age 0.1 (a), 0.2 (b), 0.3 and older (c) immature chum salmon and their average fork length (d) in the autumn of 2002-2004.
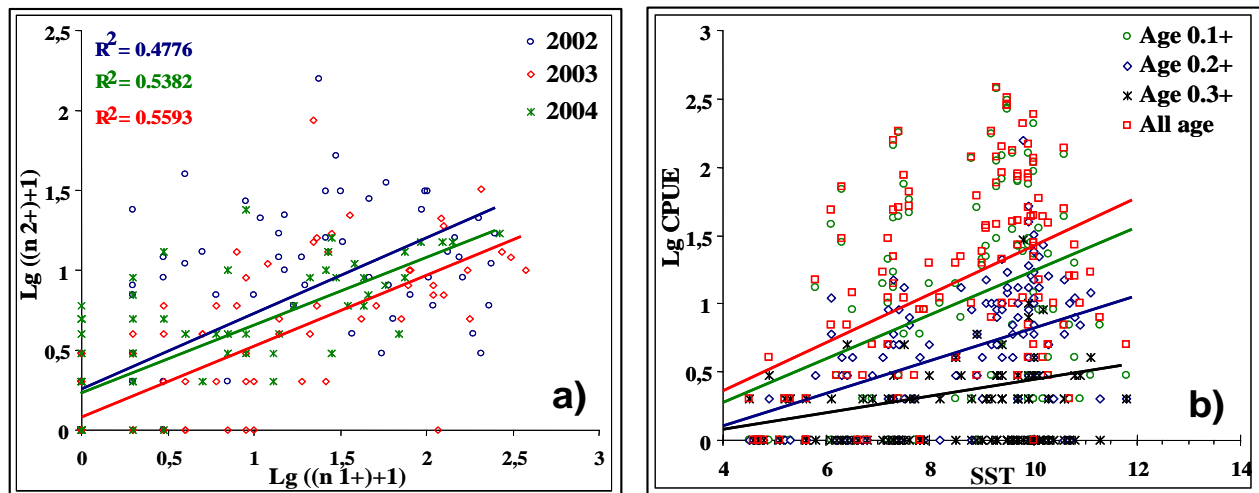
Fig. 4. Correlation between normalized CPUE values for age 0.1 and 0.2 immature chum salmon (a) and between normalized CPUE values for immature chum salmon and sea surface temperature (SST)(b), 2002-2004. Values of correlation coefficients are significant at 95% (r = 0.69-0.75, p < 0.01).
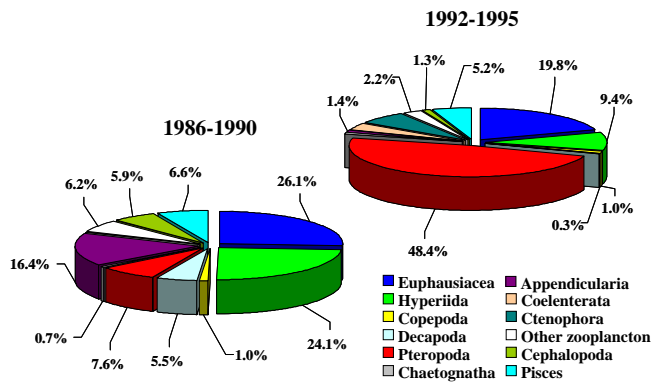
Fig. 5. Average diet composition of chum salmon (excluding juveniles) in the Commander Basin during autumn in 1986-1990 and 1992-1995.
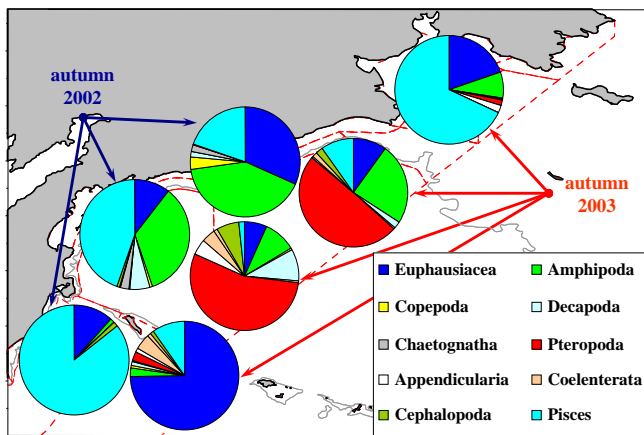
Fig. 6. Average diet composition of chum salmon (excluding juveniles) in the western Bering Sea during autumn 2002 and 2003.

Table 3. Trophic relationships of chum salmon in the western Bering Sea during summer 1995 and 2003.

Prey organisms	Consumption of prey (thousand tons)	
	Summer 1995	Summer 2003
Euphausiids	79.2	336.8
Amphipods (Hyperiids)	15.5	353.7
Copepods	4.4	0.2
Decapods	1.0	82.8
Pteropods	195.7	230.7
Gelatinous zooplankton	76.3	214.6
Fish + squids	15.7	385.4
Other	27.0	93.1
Total	415.3	1831.7
Biomass of chum (thousands of tons)	186.6	749.0

planktonic organisms such as pteropods, euphausiids and hyperiids in the deepwater Bering Sea regions (Fig. 6). In the shallow coastal areas, nektonic animals, primarily fish dominated in the chum salmon diet. For example, juvenile walleye pollock, capelin (*Mallotus villosus*) and sand lance (*Ammodytes hexapterus*) were favorite prey in Anadyr Bay and shelf areas. Though food habits of chum salmon varied from region to region, they tended to prefer pteropods and hyperiids, even when their abundance in the plankton was low. Chum salmon also frequently feed upon gelatinous planktonic animals, such as medusas, ctenophores, salps and appendicularians. These gelatinous animals are most frequently present in the diet of large (mainly maturing) chum salmon in coastal areas, while in deepwater areas, these animals account for less than 5.3–7.4% of the fish diet.

Nektonic and planktonic communities of the Bering Sea have experienced considerable changes recently, and as a result, the impact of abundant fish species on plankton resources has also changed. For example, in the 1980s the total amount of zooplankton consumed by fish, including salmon, reached 10.5 million tons only during autumn, and dropped down to 2.4 million tons in the 1990s, resulting in an increase in food supply.

The ratio between standing crop of macroplankton and fish biomass increased tens of times, compared to the 1980s: from 7.0 and 9.5 (in 1986 and 1987) to 45.3 and 80.9 (in 2000 and 2002). This parameter was even greater in autumn 2002, when the combined amount of forage zooplankton consumed by fish was assessed at 10.2 million tons. It is worth noting here that, in these years Pacific salmon accounted for 2–9% of the total amount of plankton consumed by all fish. Salmon consumed 218 thousand tons of forage zooplankton in the mid-1980s, and 234 thousand tons in the early 1990s. In autumn 2002, the biomass of forage zooplankton consumed by salmon increased more than three times and amounted 806 thousand tons, of which 479 thousand tons or 4.7% were accounted for by chum salmon. In contrast, walleye pollock consumed 87, 61 and 44% of all forage resources consumed by all fish in 1986, 1990 and 2002, respectively, in the western Bering Sea.

Chum salmon occurred in increased numbers in summer 1995 and in summer 2003. Total amount of zooplankton and nekton consumed by chum salmon in 2003 was more than four times greater than in 1995 (Table 3). In these years, chum salmon preyed predominantly upon pteropods, euphausiids and hyperiids. Gelatinous organisms (medusas and ctenophores) also were important, and in summer 1995, they were the third most important prey in the chum salmon diet after pteropods and euphausiids. In summer 1995, maturing individuals accounted for 70% of the total chum salmon biomass, while in summer 2003, immature fish accounted for 90% of the species biomass. We have already mentioned that maturing fish were more selective in cropping gelatinous organisms. These observations were supported by data collected in summer 1995.

Even in years of highest stock abundance chum salmon

consumed much less food than walleye pollock, whose annual consumption rate was assessed at 4.5–9.2 million tons in the 1980s and 1990s. As a result, the influence of chum salmon on the flow of energy (or forage resources) in the Bering Sea ecosystem is not substantial because chum salmon biomass and consumption of plankton are much smaller than those of pollock. In addition, chum salmon are known for their wide trophic flexibility, and consume both planktonic and nektonic animals. These results indicate that the recent speculations that salmon exceeded carrying capacity in the North Pacific Ocean may not be correct. Furthermore, chum salmon daily rations were high even in 2003, when the species abundance was the highest, supporting the idea that there was plenty of food for chum salmon and prey availability was far below the critical level.

CONCLUSIONS

We believe that high abundance of Pacific salmon, particularly chum salmon in the 2000s, compared to the 1980s and 1990s, in the western Bering Sea was associated with favorable forage conditions, particularly, with the high standing crop of planktonic resources in the Russian waters. However, Pacific salmon abundances and trends in their abundance are related to changes in global climate-oceanographic processes. Salmon stocks have persisted at a high level for about 20 years, and we expect a decline in their abundance in the near future. In years of high abundance, chum salmon occur both in offshore and coastal areas. In years of large abundances and increased aggregations of forage zooplankton chum salmon are forced out of the deepwater Commander Basin into areas with lower carrying capacity. At lower stock abundances, chum salmon aggregate in areas with optimal forage conditions. Thus the spatial structure of a species is related to species abundances in a manner that reduced density-dependent competition for food.

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Trends in Abundance and Biological Characteristics for North Pacific Sockeye Salmon

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Abstract: Trends in abundance, productivity, and average size were reviewed for sockeye salmon populations from Washington, British Columbia, southeast Alaska, central Alaska, western Alaska, and Russia. Aggregate catch estimates were reasonable indicators of overall stock status, but in areas toward the southern extent of their range, population-specific return and escapement estimates are also needed by fishery managers. Sockeye abundance in Russia and western and central Alaska declined coincident with a regime shift in 1949. Declines also occurred in the eastern North Pacific although they were less severe. Abundance increases were ubiquitous around the time of the regime shift in 1977. Short-term reductions in abundance in western Alaska and parts of central Alaska followed the 1989 shift but were not evident in Russia or the eastern North Pacific. The status of many North American stocks recently declined, with severest declines in southernmost areas. Trends in survival rate indices were similar to trends in catch and abundance. Average body size was inversely related to aggregate abundance, implying that growth was density-dependent. The coherence in trends in abundance, catch, and average weight among stocks suggests that large-scale environmental processes are major factors controlling sockeye salmon survival and production around the North Pacific Rim, and probably restrict the total production from particular ocean zones. However, local-scale environmental processes can result in regional differences in productivity.

Keywords: sockeye salmon, North Pacific Ocean, fish abundance, biological characteristics, regime change

INTRODUCTION

Trends in salmon abundance indices, including catch, as well as various biological characteristics, including body size and survival, have been used as indicators of climate change (Beamish and Bouillon 1993; Francis and Hare 1994; Hare and Francis 1995). These trends suggest that decadal-scale shifts in abundance of sockeye salmon (*Oncorhynchus nerka*) and other species of salmon have occurred over broad areas of the North Pacific Rim (Beamish and Bouillon 1993; Francis and Hare 1994; Hare and Francis 1995). Periods or regimes of intense winter-time Aleutian lows correlate with increased zooplankton abundance in the Subarctic Gyre (Francis and Hare 1994; Brodeur and Ware 1992). High productivity in the Subarctic Gyre during regimes of intense winter-time Aleutian lows appears to result from increased water column stability associated with reduced salinities and high precipitation that characterize these regimes (Gargett 1997).

Eleven of these regime shifts have occurred in the North Pacific Ocean since 1650 (Gedalof and Smith 2001), with recent shifts occurring in 1949, 1977, 1989 (Francis and

Hare 1994; Hare and Mantua 2000; Beamish and Bouillon 1993), and possibly 1998 (Peterson and Schwing 2003). It is now widely accepted that these shifts are responsible for large changes in the abundance of many species of fish (Bakun and Broad 2002; Trites et al. 2007), including Pacific salmon.

Researchers (e.g. Beamish et al. 1999) have hypothesized that the North Pacific Ocean alternates between high and low salmon production regimes that are driven by decadal-scale changes. In 1949, there was a shift from a high to a low production regime (Francis and Hare 1994; Hare and Francis 1995; Beamish and Bouillon 1993); in 1977 conditions shifted back to a high production regime (Francis and Hare 1994; Hare and Francis 1995; Beamish and Bouillon 1993; Hare and Mantua 2000), and in 1989, back to a low production regime (Hare and Mantua 2000).

Catches of large aggregates of salmon vary in synchrony with oceanographic indices (Beamish and Bouillon 1993; Beamish et al. 1999; Beamish and Noakes 2002). In addition, decreases in salmon body size coincident with increases in salmon abundance and climatic changes have been widely observed (Bigler et al 1994; Helle and Hoffman 1998;

Walker et al. 1998; Pyper and Peterman 1999). The spatial and temporal scale for these patterns of salmon abundance suggests climate forcing and bottom-up control of salmon abundance.

However, some researchers argue that local processes are more important than large-scale climate processes in determining the survival of salmon at sea (Pyper et al. 2001; Mueter et al. 2002a). Patterns of covariation in survival (i.e. from stock-recruit analysis) between Bristol Bay and Fraser River sockeye salmon stocks (Peterman et al. 1998) and among Washington, British Columbia and Alaska pink (*O. gorbuscha*), chum (*O. keta*), and sockeye salmon stocks (Pyper et al. 2005) are correlated on both local and regional spatial scales. Catches of northern and southern populations of salmon can be out of phase with each other (Hare et al. 1999).

In this review we examine trends and patterns of covariation of abundance (catch and escapement), survival, and body size for sockeye salmon stocks in the North Pacific. We consider the two competing hypotheses of salmon population regulation: 1, ocean basin-scale environmental processes control sockeye salmon production, and 2, local- and regional-scale environmental processes control sockeye salmon production. While others (e.g. Peterman et al 1998;

Mueter et al 2002) have carried out similar analyses, our data set is much larger, both in terms of number of populations and the area covered.

METHODS

Data Sources

We examined spatial abundance patterns and biological characteristics for sockeye salmon populations in the following areas: Russia, Bristol Bay, Alaska Peninsula, south Alaska Peninsula, Chignik, Kodiak, Cook Inlet, Prince William Sound, southeast Alaska – northern British Columbia (BC), and southern BC – Washington (Fig. 1). Southeast Alaska and northern BC were combined because of the significant contribution of northern BC stocks to fisheries in southeast Alaska. Similarly, the southern BC and Washington areas were combined because sockeye salmon catches in Washington are primarily of Fraser River (southern BC) origin.

We evaluated two abundance estimates: retained commercial catch, and total run sizes (catch plus spawning escapement). We also examined trends in survival based on stock-recruit analysis of recruits from parental escapements when these data were available.
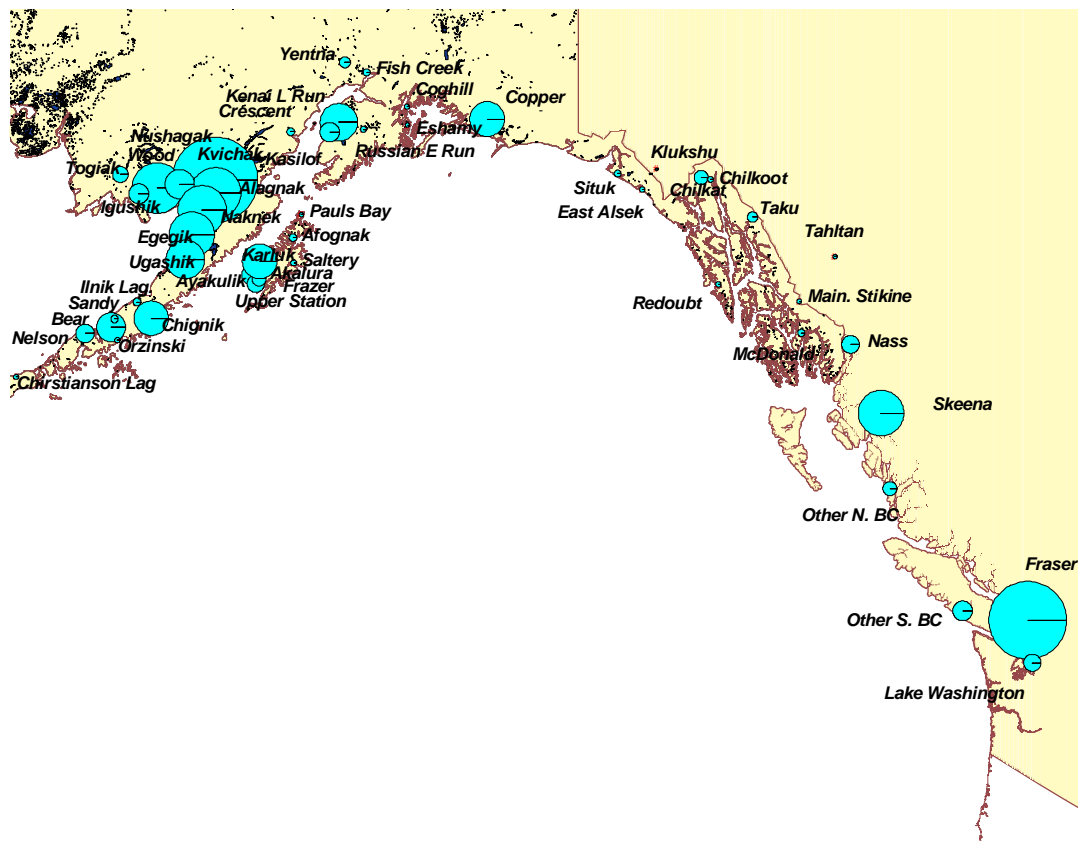
Fig. 1. Major stocks of sockeye salmon assessed in Alaska, B.C., and Washington. The size of the pie scaled to average escapement, 1996–2005.

Commercial Catch Data

Commercial catch of sockeye salmon by area were from Eggers et al. (2005), Alaska Department of Fish and Game catch records, and Fisheries and Oceans Canada (DFO) catch records (e.g. Irvine et al. 2006). Canadian data were partitioned into fish retained in commercial fisheries taking place north and south of the north end of Vancouver Island.

Escapement Data

Escapement data were assembled for each area, except that estimates were not available for Russia. In Bristol Bay, escapement has been assessed for essentially all of the sockeye-producing river systems since 1956 (Fair et al. 2004). In the Alaska Peninsula area, escapements have been estimated for most of the sockeye-producing river systems since the early 1970s (Nelson et al. 2005). In the Chignik area, escapements have been assessed annually since 1922 (Dahlberg 1968; Witteveen et al. 2005). In the Kodiak area, escapements have been estimated for three of the major systems since the 1920s, and in virtually all of the other sockeye-producing river systems since the late 1970s (Nelson et al. 2004). In the Cook Inlet area, assessment of sockeye escapement has been fairly complete since the late 1970s (Hasbrouck and Edmundson 2005). Only a portion of Susitna River (i.e., Yentna River) sockeye escapement is assessed. In Prince William Sound, the assessment of sockeye escapement is fairly complete with the exception of the Copper River Delta river systems that are incompletely assessed with aerial survey counts (Evenson et al 2005). Geiger et al. (2005) describe escapement programs in southeast Alaska.

Escapements are estimated annually for many British Columbia sockeye populations although methods vary, as do the numbers of systems evaluated annually. We obtained data from DFO's escapement database (nuSEDs) and aggregated estimates for systems north of the northern tip of Vancouver Island separately from data for systems to the south that included the Fraser River. From 1950–2004, 75–195 sockeye systems were assessed annually in northern BC (excluding transboundary rivers), and 48–290 systems in southern BC.

Run Sizes

Run sizes for each area were estimated as the sum of escapements and commercial catches in the area. Run size estimates will be biased low when non-commercial (i.e. recreational and aboriginal) fisheries occur.

Stock Recruit Data

Stock-recruit data from brood tables based on age-specific total runs (catch plus escapement) were assembled for 32 sockeye salmon stocks (Appendix 1). Fewer stocks had stock-recruit data than escapement data because stock and age-specific catch estimates are not available for many stocks. We restricted our analysis to those stocks that had a time series of spawner numbers that we judged had been estimated with reasonable precision. Except for Russia, there were at least two stocks with stock-recruit data from each area. To avoid errors in catch allocations implicit in the individual river system (population) brood tables, we pooled these data for those populations common to major commercial fisheries. For instance, in Bristol Bay we analyzed data for 3 stocks (Togiak; Nushagak District (pooled brood tables for Wood, Igushik, and Nushagak); and Eastside Districts (pooled brood tables of Kvichak, Alagnak, Naknek, Egegik, and Ugashik (Appendix 1; Fair et al. 2004). We analyzed data for 2 stocks in the Alaska Peninsula area (Bear River late-run, and Nelson Lagoon (Nelson et al. 2005)), 2 stocks in the Chignik area (Chignik early-run, Chignik late-run (Witteveen et al. 2005)), 4 stocks in the Kodiak area (Ayakulik, Upper Station early-run, Upper Station late-run, Karluk combined-run, and Frazer (Nelson et al. 2004)), 4 stocks in the Cook Inlet area (Kenai late-run, Russian R early-run, Kasilof, and Crescent (Hasbrouck and Edmondson 2005)), 3 stocks in the Prince William Sound area (Eshamy, Coghill, Copper (Evenson 2002; Evenson et al. 2005)), 9 stocks in southeast Alaska – northern British Columbia (Situk, Italio, Klukshu, East Alsek, Chilkat, Chilkoot, Redoubt, Nass, Skeena (Geiger et al. 2005; DFO, Nanaimo, BC, unpublished data)) and 5 stocks in the Fraser River watershed (Birkenhead, early Stuart, early Summers, Summers, and late Summers (Schubert 1998)).

As previously mentioned, methods to estimate escapements vary (Appendix 1). Visual surveys from towers are the predominant method in Bristol Bay; weirs are commonly used in the Alaska Peninsula, Chignik, and Kodiak. Weirs and sonar are the most common techniques in Cook Inlet and Prince William Sound while aerial visual surveys, mark-recapture, and weirs are common in southeast Alaska.

Within Canada, in the Nass fishwheel (formerly gillnet) test fishery catches are calibrated with sockeye counts at a fishway below Meziadin Lake (Link and Peterman 1998). In smaller Nass tributaries, visual survey estimates are expanded using the area-under-the-curve method (Levy 2006). In the Skeena, a test fishery in the lower river is calibrated with fence counts at Babine Lake (DFO 1999). Visual surveys are carried out in various Skeena tributaries and a weir is maintained on the Sustut. In the Fraser, the method used depends on the anticipated size of the run, and since populations can have strong and weaker cycle lines, methods for some systems vary among years. For most of the time series, when anticipated escapements were less than 25,000, estimates were usually generated by visual surveys and when anticipated escapements exceeded 25,000, estimates were made using counting fences (weirs) and mark-recapture (Schubert 1998). Appendix 1 lists the Fraser escapement estimation methods used in 2004 (K. Benner, Fisheries and Oceans Canada, 985 McGill Place, Kamloops BC V2C 6X2,

pers. comm.). Fraser stock groups (Birkenhead, early Stuart, early Summers, Summers, and late Summers) are separated primarily based on run timing. Fraser visual survey estimates usually are indexed peak live counts plus cumulative dead and carcass counts and are generally complete.

Catch Weight Data

Average weight of sockeye salmon in the catch by area was based on the reported catch in weight divided by the reported catch in numbers of fish. Data for the Alaskan areas, 1960 to 1966 were from INPFC (1979), 1977–2004 data were from Alaska Department of Fish and Game catch records. Data for northern and southern British Columbia, 1960–2004 were the reported catch in weight from purse seine gear divided by the reported catch in numbers from purse seine gear from DFO catch records.

Statistical Analyses

Using methods in Peterman et al. (1998), we calculated indices of survival for the 32 stocks with stock recruit data after normalizing the data and removing possible within-stock density dependence. We fit the Ricker stock recruit model (Ricker 1975) to each data set by maximum likelihood with lognormal process error (Microsoft Excel Solver). The index of survival was the time series of brood-year residuals (i.e., ln(observed recruits/predicted recruits)) with predicted recruits based on the fitted Ricker stock-recruit model.

We tested for trends in catch time series by area, abundance (commercial catch plus escapement) by area, survival rate index by stock, and catch weights by area. To evaluate spatial coherence, we computed correlations among areas and stocks for the time series.

Many of these time series were highly auto-correlated. Here the test of significance of the correlation coefficient would have a type one error rate greater than the assumed alpha. To correct for the tendency of two auto-correlated time series to appear correlated, we used the method outlined in Peterman et al. (1998) (who cited results of Pyper and Peterman (1998)) to adjust the degrees of freedom in all our tests of significance for correlation coefficients.

To improve the ease of visually interpreting time series plots, we computed running averages over the average lifespan of the fish (4 years for southern BC and 5 years for the rest). This procedure reduces year-to-year fluctuations in abundance that may have little influence on overall population status.

RESULTS

Catch

Sockeye salmon occur throughout the North Pacific Rim, from west Kamchatka on the west to the Columbia River in the southeast (Fig. 1).   The largest runs are in the Bristol Bay area (Appendix 1), with the recent 10-year average Bristol Bay catch of 21 million, which is roughly 40% of the North Pacific total. The recent 10-year average catch and proportion of the North Pacific is 5.8 million and 11% for Russia, 3.8 million and 7.1% for the Alaska Peninsula, 1.5 million and 2.8% for Chignik, 3.5 million and 6.8% for Kodiak, 3.3 million and 4.4% for Cook Inlet, 2.3 million and 4.4% for Prince William Sound, 3.7 million and 7% for southeast Alaska – northern BC, and 2.2 million and 4.1% for southern BC - Washington.

Catches in western Alaska (Bristol Bay and Alaska Peninsula) from the 1920s to the late 1940s fluctuated with no discernible trend, then remained relatively low until the early 1970s (Fig. 2).   Catches increased rapidly following the 1977 regime shift and subsequently declined in the late 1990s. The pattern of sockeye catch in Russia was similar, except the increase from the early 1970s lows was moderate and delayed relative to catches in western Alaska, and there was no indication of reduced Russian catches in the 1990s.

The pattern of catch in all central Alaska areas was similar to that of western Alaska. For the Chignik, Kodiak, and Cook Inlet areas, declines in catch occurred during the 1990s, similar to those observed in western Alaska (Fig. 2). No decline in catch in the 1990s occurred in Prince William Sound.

Sockeye salmon catches in the eastern North Pacific Alaska, 1925–1950, were compiled for southeast Alaska and combined BC and Washington State areas. Thereafter, catches were compiled for combined southeast Alaska and northern BC and for the combined southern BC and Washington State. Southeast Alaska catches declined around the time of the 1949 regime shift while BC and Washington catches were relatively constant until the late 1970s (Fig. 2). Catches subsequently increased until the mid-1990s after which they declined precipitously.

We examined patterns of co-variation of salmon catches among the 9 areas using correlation analysis. There was strong positive correlation in sockeye salmon catch among the areas (mean correlation = .433) with 35 of 36 possible 2-way correlations being positive and 15 being significant ($\alpha = 0.10$) (Table 1). Correlations were generally the highest for adjacent areas, and decreased with increasing distance, indicating substantial spatial coherence in catches.

Body Size

Trends in body size (average weight) were similar in many areas (Fig. 3). Size increases were common from the 1960s through the late 1970s, followed by decreases during the early 1990s, and increases during the last decade (Fig. 3). Exceptions to this general pattern included sockeye from southern BC that exhibited little discernible temporal pattern other than a short-lived decrease in size in the early 1990s, and sockeye from Bristol Bay, the Alaska Peninsula, south-
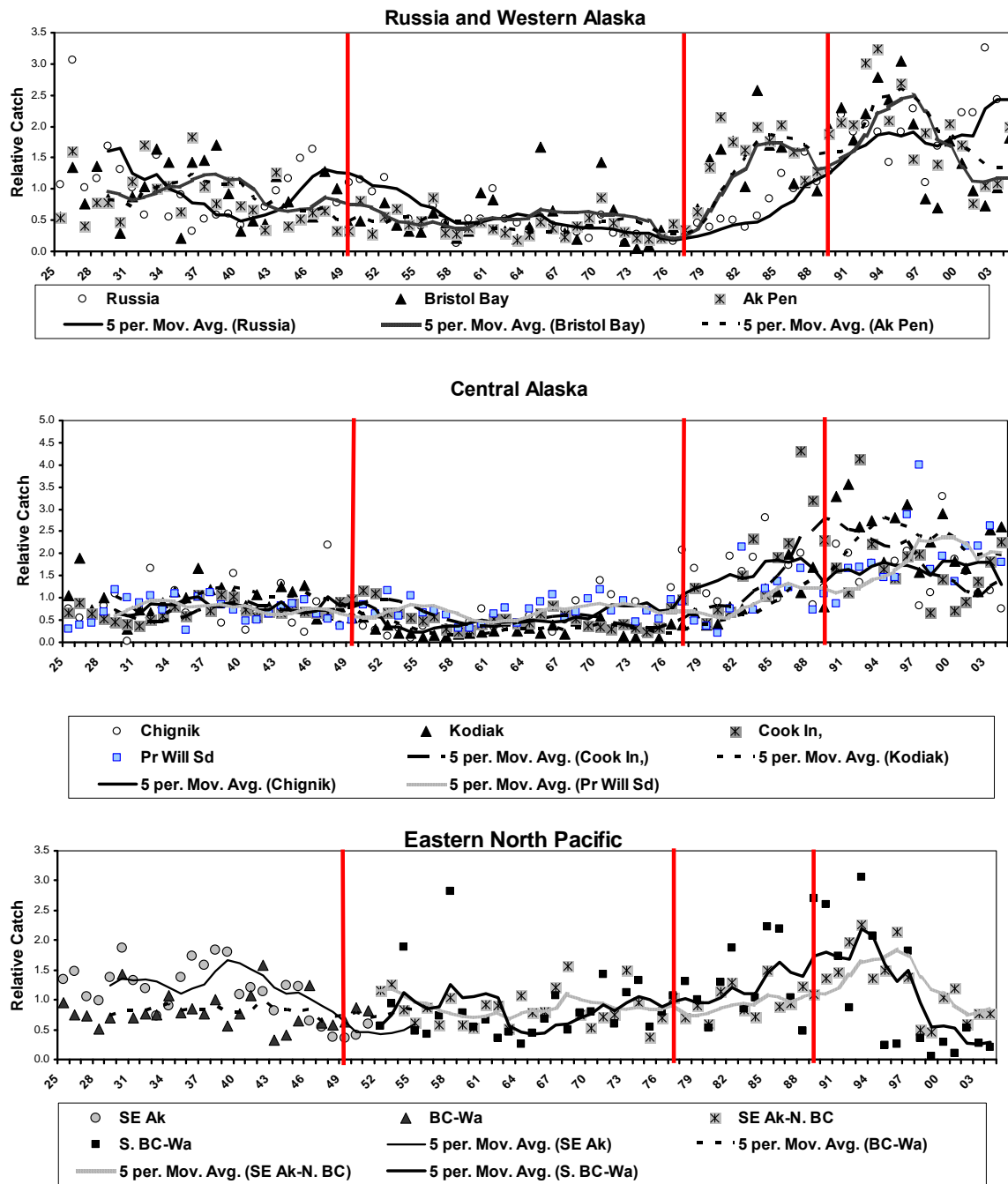
Fig. 2. Historical trends in sockeye salmon catch by area. Catches are in numbers scaled to historical averages. Vertical lines at 1949, 1977, and 1989 separate the regimes.

east Alaska and northern British Columbia where sizes have been relatively constant since the late 1970s.

In Bristol Bay and the Alaska Peninsula, significant stock-specific variations in age-at-maturity occur. In Bristol Bay, Kvichak River salmon are the dominant population that returns primarily at ocean age 2 (.2). Because of the cyclic nature of Bristol Bay runs, this masks trends in average size. Estimates of the mean length of the major ages-classes in the Bristol Bay total run are available (West and Fair 2006).

There appeared to be minor length increases for each age-class from the mid 1950s through the late 1970s, then decreases through the early 1990s, followed by increases commencing in the early 1990s (Fig. 4). These patterns appeared most pronounced for ocean age-two classes (Fig. 4).

We examined the patterns of co-variation in body size among the nine areas. There was a strong positive correlation in sockeye salmon body size among the areas (mean correlation = .433) with 36 of 36 possible 2-way correlations

Table 1. Pairwise correlation coefficients of sockeye salmon catch, 1925–2004, in various areas from Russia to British Columbia - Washington. Correlation coefficients that are statistically significant at α = 0.05 are heavily shaded and coefficients significant at α = 0.10 are lightly shaded.

	Russia	Bristol Bay	Alaska Peninsula	Chignik	Kodiak	Cook Inlet	Prince William Sound	SE Alaska - N. British Columbia	S. British Columbia - Washington
Russia	1								
Bristol Bay	0.459	1							
Alaska Peninsula	0.498	0.848	1						
Chignik	0.331	0.603	0.614	1					
Kodiak	0.714	0.667	0.738	0.565	1				
Cook Inlet	0.444	0.603	0.622	0.413	0.563	1			
Prince William Sound	0.516	0.356	0.492	0.391	0.586	0.498	1		
SE Alaska - N. British Columbia	0.325	0.428	0.486	0.235	0.461	0.430	0.358	1	
S. British Columbia - Washington	-0.057	0.224	0.307	0.138	0.106	0.205	0.026	0.379	1
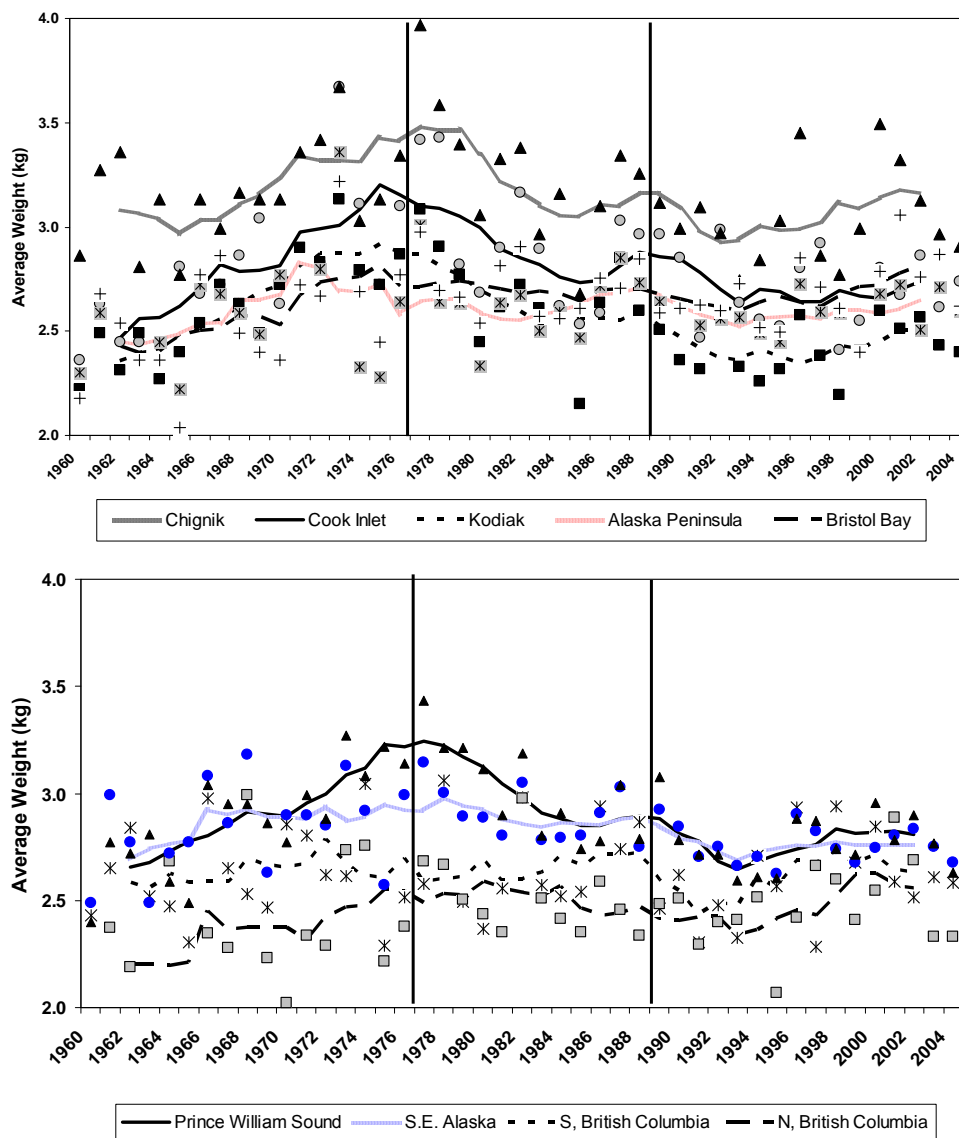
Fig. 3. Average body size and trend of sockeye salmon in the commercial catch, 1960–2004. Upper panel shows trends for Chignik, Cook Inlet, Kodiak, Alaska Peninsula, and Bristol Bay areas. Lower panel shows trends for Prince William Sound, southeast Alaska, southern British Columbia, and northern British Columbia areas. Vertical lines at 1949, 1977, and 1989 separate the regimes.
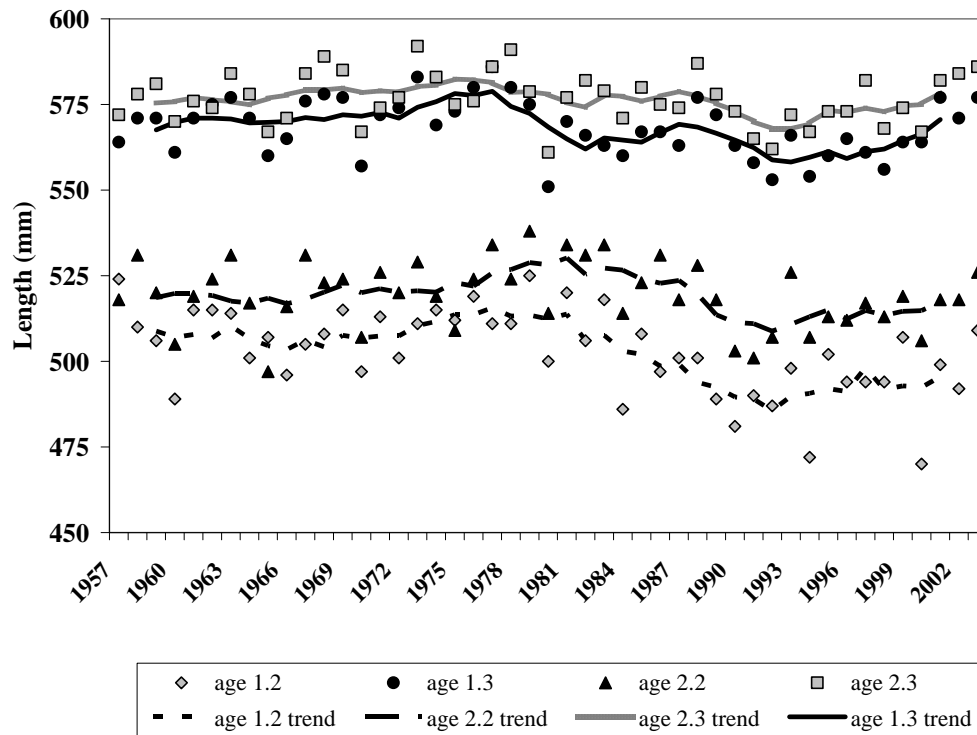
Fig. 4. Average body length and trend for returning Bristol Bay sockeye salmon, 1957– 2003.

Table 2. Pairwise correlation coefficients in average weight of sockeye salmon in the catch among areas, 1960 to 2004, in areas from southern British Columbia to Bristol Bay. Correlation coefficients that are statistically significant at α = 0.05 are heavily shaded and coefficients significant at α = 0.10 are lightly shaded.

	Year	Southern BC	Northern BC	S.E. Alaska	Prince William Sound	Cook Inlet	Kodiak	Chignik	Alaska Peninsula	Bristol Bay
Year	1.000									
Southern BC	0.005	1.000								
Northern BC	0.304	0.256	1.000							
S.E. Alaska	-0.165	0.381	0.599	1.000						
Prince William Sound	-0.124	0.205	0.436	0.658	1.000					
Cook Inlet	-0.032	0.161	0.462	0.625	0.711	1.000				
Kodiak	-0.238	0.277	0.280	0.637	0.798	0.773	1.000			
Chignik	-0.150	0.327	0.360	0.600	0.693	0.621	0.762	1.000		
Alaska Peninsula	0.094	0.328	0.366	0.631	0.472	0.559	0.623	0.667	1.000	
Bristol Bay	0.332	0.333	0.566	0.536	0.542	0.516	0.515	0.565	0.771	1.000

being positive and 34 being significant (α = 0.10) (Table 2). The highest correlations were among adjacent areas, with correlations decreasing with increasing distance. Body size in southern British Columbia showed the least coherence with other areas (Table 2).

Abundance

In Bristol Bay escapements generally co-varied with total runs until the early 1980s (Fig. 5). Since then, escapements have been relatively constant, a result of the constant escapement harvest policy under which the fisheries have been managed. Total runs for Bristol Bay sockeye salmon increased after the 1977 regime shift (Fig. 4) but not to the extent that catch increased. This is due to the relatively greater exploitation of large runs that have occurred in Bristol Bay since the late 1970s. Total runs declined in the late 1990s but are still large relative to those prior to the late 1970s (Fig. 5).

Trends in total runs and escapements of sockeye salmon in the northern Alaska Peninsula area are similar to that of Bristol Bay. Escapements co-varied with total runs before
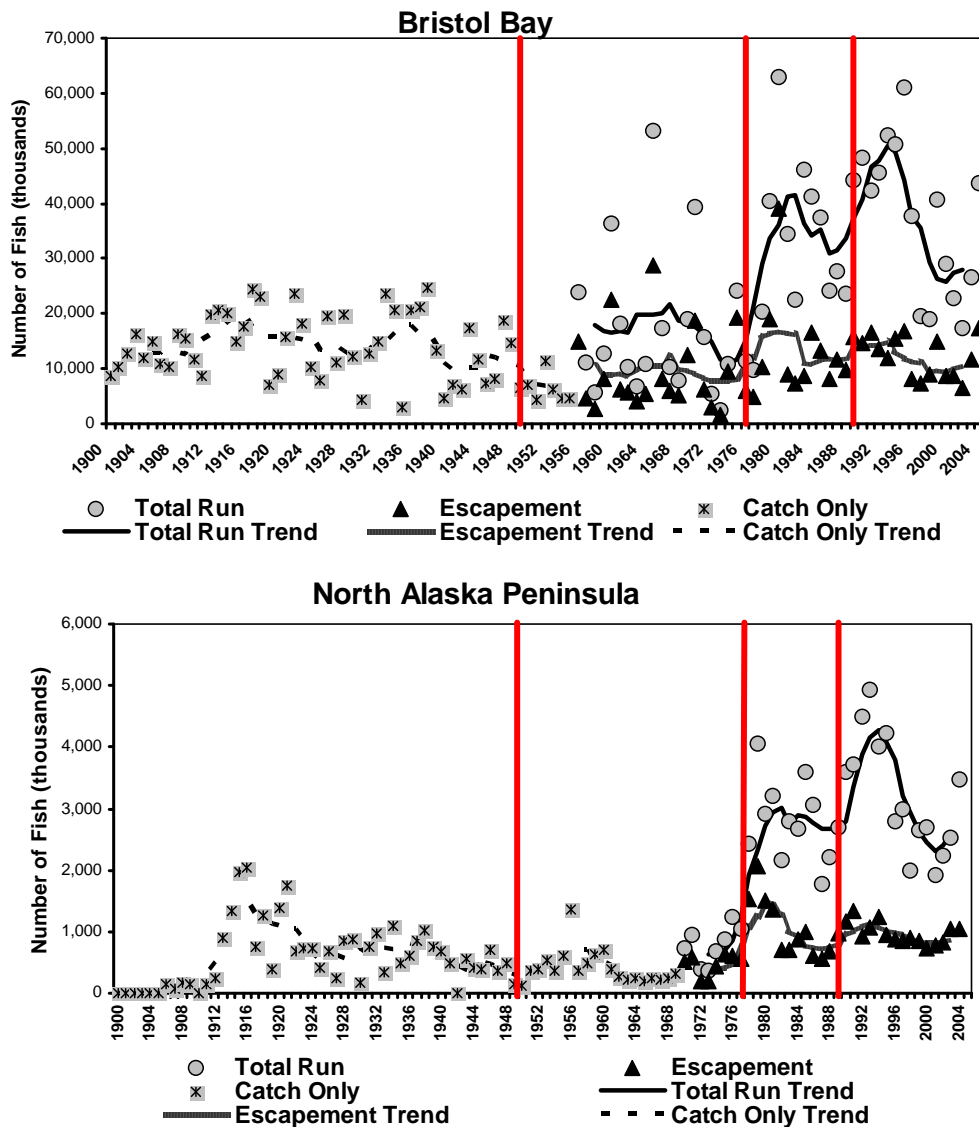
Fig. 5. Trends in total run (catch + escapement), escapement, and catch (prior to 1956) of sockeye salmon in Bristol Bay (upper panel). Trends in total run (catch + escapement), escapement, and catch (prior to 1970) of sockeye salmon in the northern Alaska Peninsula (lower panel). Vertical lines at 1949, 1977, and 1989 separate the regimes.

the early 1980s and have been relatively constant since (Fig. 5). The relative increase in north Alaska Peninsula sockeye salmon runs appears to be greater than that of Bristol Bay; however, escapements were not monitored prior to 1970.

Chignik River escapements also fluctuated with catch until the early 1980s, and have been relatively constant since (Fig. 5). Escapements were much more variable during the period of federal management before the State of Alaska took over management in 1960. With state management, and timely escapement with the Chignik weir close to the fishery, managers have been able to effectively control fishing and to consistently achieve escapement targets in the Chignik fishery. After 1960, escapements were more stable, and generally increased with the increasing runs through the 1970s. With the larger runs since the late 1970s, escapements have

been maintained at maximum sustained yield levels. Total runs of sockeye salmon to the Chignik areas decreased after the 1949 regime shift, and increased after the 1977 regime shift. Total runs were consistently high after 1977 (Fig. 6).

Escapements of sockeye salmon in the Kodiak area have been partially monitored since the 1920s, with the establishment of counting weirs on the Karluk, Akalura, and Ayakulik river systems. In the 1960s counting weirs were also established on the Upper Station and Frazer River systems. In the late 1970s, counting weirs were established on several minor river systems. Sockeye salmon escapement monitoring has been complete since the late 1970s; however a large portion of the escapement is from river systems which have been monitored since the 1920s. As with the other areas in western and central Alaska, escapements fluctuated with
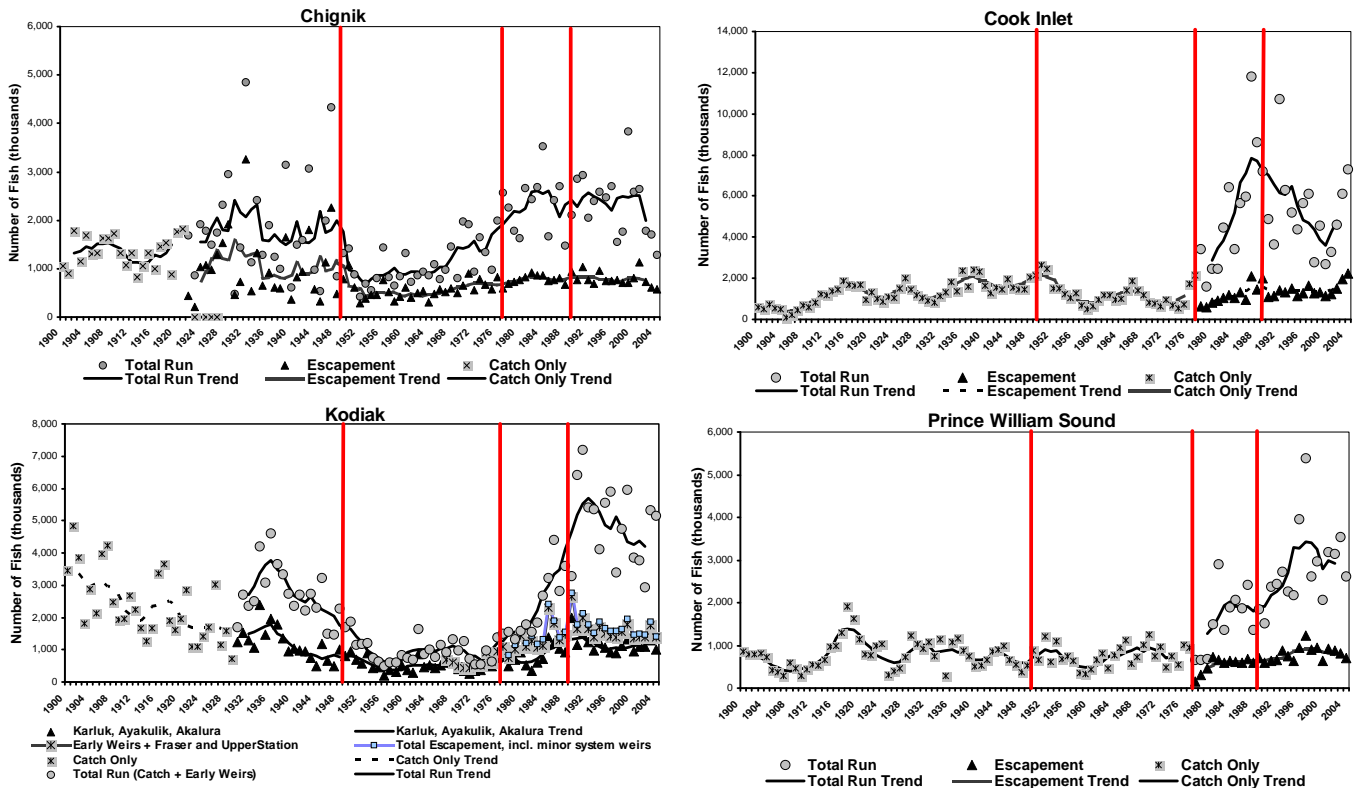
Fig. 6. Trends in total run (catch + escapement), escapement, and catch only (prior to 1922) of sockeye salmon in the Chignik Area (upper left panel). Trends in total run (catch + escapements), escapement, and catch only (prior to 1930) of sockeye salmon in the Kodiak Area (lower left panel). Trends in total run (catch + escapements), escapement, and catch only (prior to 1930) of sockeye salmon in the Cook Inlet Area (upper right panel), and Prince William Sound Area (lower right panel). Vertical lines at 1949, 1977, and 1989 separate the regimes.

catch until the early 1980s, and since have been relatively stable. Total runs of sockeye salmon to the Kokiak area decreased after the 1949 regime shift, and increased after the 1977 regime shift. Total runs to the Kodiak area increased coincident with the 1989 regime shift (Fig. 6).

Sockeye salmon escapements in Cook Inlet have been monitored since the late 1970s with establishment of sonar counting on the Kenai, Kasilof, Crescent, and Yentna river systems. Escapement monitoring is relatively complete, except that some sockeye salmon stocks in the Susitna River system are unmonitored. Sockeye salmon escapements in Cook Inlet have been relatively stable (Fig. 6). Total runs of sockeye salmon to Cook Inlet increased coincident with the 1977 regime shift and have continued at high levels since the mid 1980s.

Sockeye salmon escapements in Prince William Sound (except for small stocks in the Copper River delta) area have been monitored since the late 1980s with the establishment of sonar counting on the Copper River, and counting weirs on the Eshamy and Coghill rivers. Escapements have been relatively stable during this period (Fig. 6). Total runs of sockeye salmon to the Prince William Sound area increased coincident with the 1977 regime shift and have remained high since the mid 1980s.

Aggregate sockeye salmon escapements in northern BC, since 1950, are shown in Fig. 7. Most of the sockeye salmon in northern British Columbia are from the Nass and Skeena river systems (Appendix 1). Escapements trended upwards slightly from the 1950s to the mid 1980s, and subsequently declined. Sockeye salmon escapements from southeast Alaska, including transboundary rivers (i.e., Alsek, Taku, and Stikine) have been available since early 1980s. The combined escapement from the northern British Columbia and southeast Alaska areas has been decreasing since the mid 1980s. Total combined runs to southeastern Alaska/northern BC were relatively stable from the 1950s through the late 1970s, increased slightly through the mid 1990s, and have since decreased.

Aggregate sockeye salmon escapements in southern BC (Fig. 7) consist largely of Fraser River fish (Appendix 1). Escapements were relatively stable from the 1950s to the early 1980s. Escapements increased through the early 1990s as did total run sizes. Aggregate escapements in southern BC remained relatively high during the most recent decade in spite of reduced catches (Fig. 5) and consequently total run sizes (Fig. 7). Escapement estimates were significantly positively correlated with the numbers of streams surveyed in both northern and southern BC.

Southeast Alaska - Northern British Columbia

Southern British Columbia - Washington
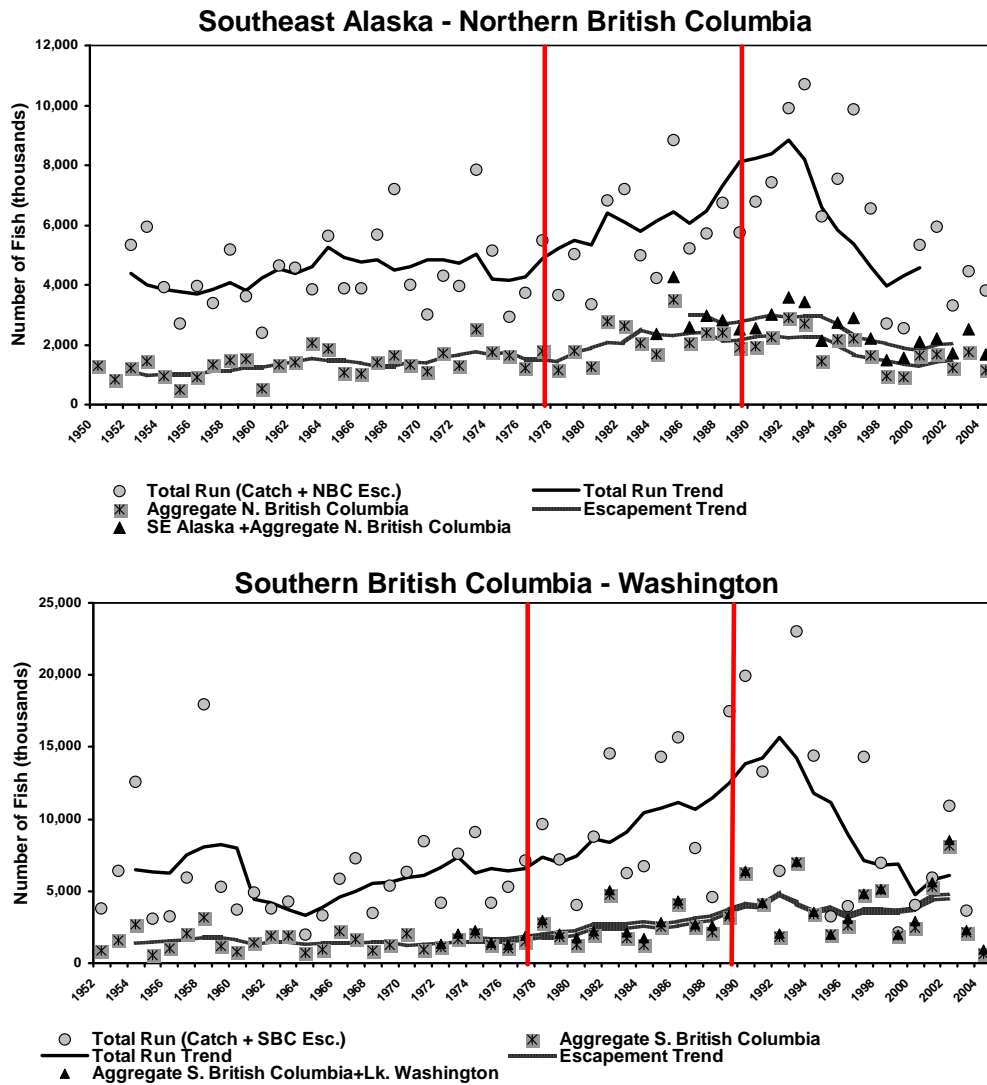
Fig. 7. Trends in total run (catch + northern British Columbia escapement) and escapement of sockeye salmon in the southeast Alaska – northern British Columbia area (upper panel). Trends in total run (catch + southern British Columbia escapement) and escapement of sockeye salmon in the southern British Columbia – Washington area (lower panel). Vertical lines at 1949, 1977, and 1989 separate the regimes.

Although the period of escapement monitoring varies by areas, monitoring has been continuous once the escapement assessment programs were implemented. Correlations of catch and escapement as well as catch abundance were examined to test whether or not catch is a good surrogate for abundance for these areas. Catch and total run were highly correlated in all areas. Catch and escapement were also highly correlated, less so than catch and total run (Table 3). Sockeye catch appears to be a reasonable surrogate for abundance, at least at the level of population aggregation we looked at here.

We also examined patterns of co-variation of salmon abundance (i.e. total run) among the 8 areas using correlation analysis. There was generally positive correlation in sockeye salmon abundance among the areas (mean correlation = .24) with 22 of 28 possible 2-way correlations being positive and 13 being significant ($\alpha = 0.10$) (Table 4). Correlations were highest for adjacent areas, and decreased with increasing distance. This indicated substantial spatial coherence in sockeye salmon total runs. Note that the high auto-correlation in the catch time series contributed to the high correlations.

Survival Indices

Trends in survival indices were examined for 34 stocks of sockeye salmon relative to the 1949, 1977, and 1989 regime shifts (Table 5). If the ocean basin-scale hypothesis is true, survival indices should be highly correlated among stocks, consistently high during the pre-1949 regime (regime 1), consistently low during the 1949 to 1977 regime (regime 2), consistently high during the 1977 to 1989 regime (regime

Table 3. Correlation of catch to escapement, and catch to total run, for areas from Bristol Bay to southern British Columbia/Washington. Correlation coefficients that are statistically significant at α = 0.05 are heavily shaded and coefficients significant at α = 0.10 are lightly shaded.

	Years	Catch - Escapement	Catch - Total Run
Bristol Bay	56–04	0.497	0.927
North Alaska Peninsula	70–04	0.481	0.962
Chignik	22–04	0.384	0.888
Kodiak	30–04	0.524	0.974
Cook Inlet	78–04	0.578	0.991
Prince William Sound	78–04	0.844	0.994
Southeast Alaska - N. British Columbia	85–04	0.722	0.979
S. British Columbia - Washington	72–03	0.388	0.950

Table 4. Pairwise correlation coefficients in sockeye abundance (total run), for areas from Bristol Bay to southern British Columbia/Washington. Correlation coefficients that are statistically significant at α = 0.05 are heavily shaded and coefficients significant at α = 0.10 are lightly shaded.

	Bristol Bay	Alaska Peninsula	Chignik	Kodiak	Cook Inlet	Prince William Sound	SE Alaska - N. British Columbia	S. British Columbia - Washington
Bristol Bay	1							
Alaska Peninsula	0.775	1						
Chignik	0.513	0.340	1					
Kodiak	0.554	0.677	0.457	1				
Cook Inlet	-0.014	0.024	-0.163	0.210	1			
Prince William Sound	-0.347	-0.129	-0.031	0.403	0.223	1		
SE Alaska - N. British Columbia	0.460	0.653	-0.048	0.260	0.313	0.017	1	
S. British Columbia - Washington	0.177	0.402	0.091	0.210	0.211	0.147	0.330	1

3), and consistently low during the post-1989 regime (regime 4).

Trends in survival rate indices were highly consistent with the 1949 and 1977 regime shifts, and marginally consistent with the 1989 regime shift (Table 5). Although stock-recruit data transcending the 1949 regime shift were limited, there was a significant decrease in average survival after the 1949 regime shift for the three stocks where data were available. There also were significant increases in mean survival following the 1977 shift. Of 20 stocks with stock-recruit data transcending the 1977 regime shift, 19 of these showed an increase in survival with 14 showing a significant increase (Table 5). There were 34 stocks with stock recruit data transcending the 1989 regime shift; here 22 stocks showed a decrease in survival with 12 showing a significant decrease. Decreases in survivals were greatest for stocks in the eastern north Pacific areas.

For western Alaska stocks, survival indices increased significantly with the 1977 regime shift for 3 out of 3 stocks; however there was little change in survival with the 1989 regime shift (Fig. 8, Table 5). A significant decline in survival index was observed only for 1 (the eastside Bristol Bay river systems) out of 5 stocks.

For the Chignik and Kodiak areas there was a significant

decrease in survival index following the 1949 regime shift for 3 of 3 stocks (Fig. 9, Table 5); a significant increase in survival following the 1977 regime shift for 5 of 7 stocks (Fig. 8, Table 5); and little change in survival following the 1989 regime shift with a decline in survival observed for 1 (Upper Station late-run) of 7 stocks.

For the Cook Inlet and Prince William Sound areas there were limited survival indices for the period preceding the 1977 regime shift. Survival indices increased with the 1977 regime shift for 4 of 4 stocks (Fig. 10, Table 5), however these were not statistically significant. Survival rates generally decreased for Cook Inlet and Prince William Sound sockeye stocks following the 1989 regime shift (Table 4) with 3 of 6 stocks showing significant decreases in survival.

For southeast Alaska sockeye stocks, there were no survival indices for the pre-1977 regime; however survival rates decreased for all but one southeast Alaska sockeye stock with 3 stocks showing a significant decrease following the 1989 regime shift (Table 5).

For northern British Columbia and Fraser River sockeye stocks, survival generally increased following the 1977 regime shift with 3 of 5 stocks showing significant increases (Fig. 11). Survival rates decreased following the 1989 regime shift for all British Columbia stocks, with 3 of 6 stocks

Table 5. Changes in mean survival index at various regimes at the 1949 regime shift (47 brood year (BY)), at the 1977 regime shift (74 BY), and 1989 (88 BY) for various stocks of sockeye salmon. Differences in mean survival rate indices (based on 2 sample mean difference tests) that are statistically significant at α = 0.05 are heavily shaded and differences significant at α = 0.10 are lightly shaded.

Stock	Area	1949 (47 BY) Regime Shift		1977 (74 BY) Regime Shift		1989 (88 BY) Regime Shift	
		Change in Mean Survival Rate Index	p-value	Change in Mean Survival Rate Index	p-value	Change in Mean Survival Rate Index	p-value
Togiak. R.	Bristol Bay			0.380	**0.037**	0.001	0.998
Nushagak Districts.	Bristol Bay			0.602	**0.002**	0.077	0.846
Eastside Districts	Bristol Bay			0.748	**0.000**	-0.394	**0.017**
Bear R. Late	N. Ak. Pen.					-0.012	0.483
Nelson R.	N. Ak. Pen.					0.118	0.758
Chignik R. Early	Chignik	-0.599	**0.008**	0.634	**0.003**	0.094	0.821
Chignik R. Late	Chignik	-0.356	**0.003**	0.463	**0.000**	-0.100	0.239
Ayakulik R.	Kodiak			0.406	**0.073**	-0.408	**0.081**
Upper Station R. Early	Kodiak			0.903	**0.002**	-0.042	0.434
Upper Station R. Late	Kodiak			0.762	**0.003**	-0.727	**0.002**
Frazer R.	Kodiak			0.507	**0.089**	0.157	0.852
Karluk R.	Kodiak	-0.448	**0.002**	0.401	**0.061**	0.069	0.894
Kenai Late	Cook Inlet			0.138	0.271	-0.377	**0.042**
Russian R. Early	Cook Inlet			0.314	0.227	0.046	0.934
Kasilof R.	Cook Inlet					-0.239	**0.027**
Crescent R.	Cook Inlet					-0.450	**0.025**
Copper R.	Prince William Sound			0.391	**0.058**	0.235	0.596
Cognill R.	Prince William Sound			0.443	0.145	-0.611	0.105
Situk R.	SE Ak - N. BC					0.005	0.987
Italio R.	SE Ak - N. BC					-0.427	0.131
Klukshu R.	SE Ak - N. BC.					-0.386	**0.028**
East Alsek R.	SE Ak - N. BC					-0.602	**0.022**
Chilkat R.	SE Ak - N. BC.					0.457	0.528
Chilkoot R.	SE Ak - N. BC					-1.467	**0.002**
Redoubt L.	SE Ak - N. BC					-0.698	0.126
Nass R.	SE Ak - N. BC					-0.087	0.308
Skeena R.	SE Ak - N. BC			0.162	0.229	-0.170	0.334
Birkenhead	S. BC			0.392	**0.036**	-1.090	**0.005**
Early Stuart	S. BC			-0.465	0.515	-0.665	**0.015**
Fraser Early Summer	S. BC			0.063	0.338	-0.228	0.107
Fraser Late Summer	S. BC			0.275	**0.068**	-0.143	0.307
Fraser Summer	S. BC			0.358	**0.020**	-0.504	**0.020**

showing a significant decrease (Table 5)

Our examination of patterns of co-variation in survival rate indices among the 34 stocks of sockeye salmon was similar to and used methods of Peterman et al (1998); however, we examined more sockeye salmon stocks distributed throughout Alaska and British Columbia. We found strong positive correlations in survival rate indices among Bristol Bay stocks (mean correlation = 0.584) with 3 of 3 possible

2-way correlations for the 3 stocks within Bristol Bay being significantly (α = 0.10) positive (Table 6). There were also strong positive correlations in survival rate indices among Fraser River stocks (mean correlation = 0.391) with 10 of 10 possible 2-way correlations for the 5 stocks within the Fraser being significantly positive. There was strong significant positive correlation (correlation = 0.410) in survival rate index for the two stocks in the Chignik area (Table 6).
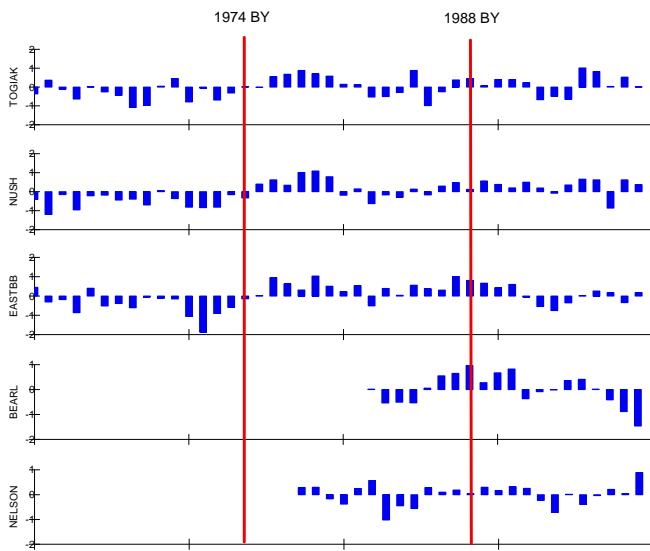
Fig. 8. Time series of standardized survival index for stocks in western Alaska, including Togiak R., Nushagak District, Eastside Bristol Bay Districts, Bear R., and Nelson R. Vertical lines separate the brood years affected by the 1977 and 1989 regime shifts. BY = brood year.
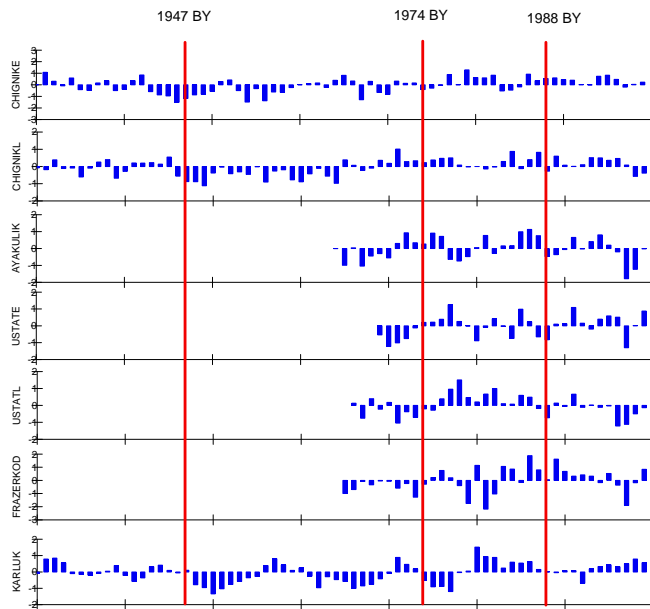
Fig. 9. Time series of standardized survival index to stocks in the Chignik and Kodiak areas, including Chignik early-run, Chignik late-run, Ayakuluk R., Upper Station early-run, Upper Station late-run, Frazer R., and Karluk R. Vertical lines separate the brood years affected by the 1977 and 1989 regime shifts. BY = brood year.

Fig. 10. Time series of standardized survival index to stocks in the Cook Inlet and Prince William Sound areas, including Kenai R. late-run, Russian R. early-run, Kasilof R., Crescent R., Copper R., and Coghill R. Vertical lines separate the brood years (BY) affected by the 1977 and 1989 regime shifts.
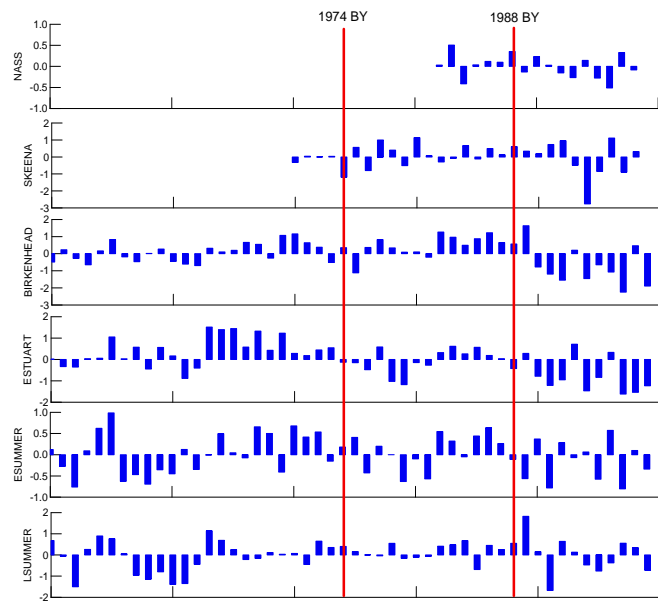
Fig. 11. Time series of standardized survival index to stocks in the British Columbia area, including Nass R, Skeena R., Birkenhead, early Stuart. Fraser River early summer-run, and Fraser R. late summer-run. Vertical lines separate the brood years (BY) affected by the 1977 and 1989 regime shifts.

For the other areas, patterns of co-variation in survival among sockeye salmon stocks within the area were generally positive; however considerably weaker than for stocks within the Bristol Bay, Fraser River, and Chignik areas (Table 6). For stocks within the Alaska Peninsula there was positive correlation (mean correlation = 0.19) with 3 of 3

possible 2-way correlations being positive with no significant correlations. For Kodiak stocks there was positive correlation (mean correlation = 0.13) in survival rate index, with 6 of 10 possible 2-way correlations being positive, 2 being significant. For stocks within the Cook Inlet area there was positive correlation (mean correlation = 0.22) in survival rate

Table 6. Pairwise correlation coefficients among survival rate (spawner to recruit) indices for sockeye salmon stocks from Bristol Bay to southern British Columbia. Positive correlation coefficients that are statistically significant at α = 0.05 are heavily shaded and coefficients significant at α = 0.10 are lightly shaded. Negative correlation coefficients that are statistically significant at α = 0.05 are in bold type.

	Bristol Bay			North Alaska Peninsula		Chignik			Kodiak				Cook Inlet			
	Togiak	Nushagak Dist.	Eastside Dist.	Bear Late	Nelson R.	Chignik Early	Chignik Late	Ayakulik	Upper Station Early	Upper Station Late	Frazer R.	Karluk R.	Kenai Late	Russian R Early	Kasilof R.	Crescent R.
Togiak	1.000															
NushagakD.	0.607	1.000														
EastsideD.	0.534	0.611	1.000													
BearLate	0.106	0.161	0.354	1.000												
NelsonR.	0.055	0.169	0.191	0.024	1.000											
ChignikEarly	0.244	0.372	0.252	0.289	0.010	1.000										
ChignikLate	0.340	0.393	0.247	0.595	-0.120	0.410	1.000									
Ayakulik	0.080	0.402	0.219	0.382	-0.061	0.126	0.303	1.000								
UpperStationEarly	0.349	0.591	0.324	-0.129	-0.063	0.336	-0.196	0.244	1.000							
UpperStationLate	-0.070	0.029	0.070	0.027	-0.295	0.284	-0.122	0.179	0.469	1.000						
FrazerR.	0.135	0.290	0.109	0.367	0.359	-0.082	0.256	0.320	0.164	0.106	1.000					
KarlukR.	-0.061	-0.105	0.156	-0.287	-0.015	0.186	0.185	0.160	-0.300	-0.074	-0.012	1.000				
KenaiLate	-0.122	-0.256	-0.082	-0.454	-0.102	-0.204	-0.239	-0.045	0.067	0.393	-0.001	0.136	1.000			
RussianR.Early	0.021	0.246	0.221	-0.065	0.276	0.089	0.022	0.364	-0.027	-0.145	0.003	0.256	-0.059	1.000		
KasilofR.	-0.333	-0.374	-0.063	-0.531	-0.352	0.117	-0.322	0.104	-0.137	0.323	-0.410	0.386	0.651	0.245	1.000	
CrescentR.	-0.061	-0.279	-0.348	-0.603	-0.298	0.043	-0.159	-0.163	-0.125	0.194	-0.312	0.288	0.321	-0.268	0.423	1.000
CopperR.	-0.146	0.016	-0.014	0.154	0.039	0.424	-0.138	-0.159	0.359	0.434	0.192	-0.060	-0.001	-0.082	-0.023	-0.303
Cognill	0.011	0.069	-0.115	-0.492	-0.220	0.098	-0.051	0.070	0.201	0.266	-0.184	-0.008	0.215	0.160	0.459	0.327
Situk	0.151	0.241	0.326	0.292	0.236	0.313	0.080	0.272	0.201	0.040	0.078	0.098	0.042	0.218	0.016	-0.392
ItalioR.	0.304	0.118	0.254	-0.097	0.133	0.124	-0.170	-0.162	-0.095	0.113	-0.178	-0.231	0.029	0.254	0.226	0.281
KlukshuR	-0.056	-0.030	0.500	0.378	0.204	0.003	-0.134	-0.135	-0.023	0.338	-0.125	-0.238	0.042	0.039	0.048	-0.298
EastAlsekR.	-0.098	-0.006	0.369	0.242	0.018	0.208	-0.256	0.098	-0.136	0.360	0.018	0.094	0.222	0.113	0.212	0.147
ChilkatR.	-0.245	0.113	-0.160	0.291	0.374	0.027	0.297	-0.023	-0.176	-0.337	0.264	-0.250	-0.343	0.053	-0.364	-0.370
ChilkootR.	0.196	-0.113	0.264	-0.249	-0.240	-0.009	0.001	-0.075	0.088	0.490	-0.187	0.181	0.503	-0.327	0.323	0.575
RedoubtR.	-0.640	-0.565	-0.118	-0.220	0.102	-0.317	-0.469	-0.068	-0.137	0.429	-0.290	0.010	0.263	0.116	0.286	-0.205
NassR.	0.119	0.223	-0.101	0.036	0.139	0.166	-0.257	-0.293	-0.274	-0.277	0.024	-0.488	-0.195	0.108	-0.017	-0.362
SkeenaR.	0.060	0.053	0.061	-0.064	0.163	0.034	-0.080	-0.104	0.020	0.062	0.278	-0.008	0.240	-0.156	0.111	-0.006
Birkenhead	-0.025	-0.040	0.076	0.336	-0.237	0.005	0.218	0.030	-0.155	0.322	0.223	0.043	0.141	-0.066	0.060	-0.005
Early Stuart	-0.253	-0.329	-0.206	0.330	-0.309	-0.266	-0.040	0.062	-0.135	-0.030	0.062	-0.223	0.083	-0.282	-0.046	-0.071
Early Summer	-0.018	0.105	-0.120	0.271	-0.093	-0.093	0.179	0.120	-0.043	-0.080	0.186	-0.088	0.104	0.007	-0.028	-0.020
Late Summer	-0.058	0.093	0.180	0.217	-0.120	-0.070	0.219	-0.250	-0.412	-0.051	0.130	-0.097	0.071	0.025	-0.091	0.052
Summer	-0.040	-0.009	0.114	0.416	-0.318	0.024	0.167	0.161	-0.107	0.236	0.093	-0.039	-0.028	-0.059	0.132	0.058

Table 6 (continued).

	Prince William Sound			Southeast Alaska/Northern BC												
	Copper	Cognill	Situk	Italio	Klukshu R	East Alsek R.	Chilkat R.	Chilkoot R.	Redoubt R.	Nass R.	Skeena R.	Birkenhead	Early Stuart	Early Summer	Late Summer	Summer
Togiak																
NushagakD.																
EastsideD.																
BearLate																
NelsonR.																
ChignikEarly																
ChignikLate																
Ayakulik																
UpperStationEarly																
UpperStationLate																
FrazerR.																
KarlukR.																
KenaiLate																
RussianR.Early																
KasilofR.																
CrescentR.																
CopperR.	1.000															
Cognill	-0.064	1.000														
Situk	-0.070	-0.106	1.000													
ItalioR.	-0.216	0.238	-0.098	1.000												
KlukshuR	0.267	-0.067	0.161	0.206	1.000											
EastAlsekR.	0.018	-0.290	-0.108	0.385	0.524	1.000										
ChilkatR.	0.474	-0.314	0.101	-0.033	0.009	-0.102	1.000									
ChilkootR.	-0.267	0.167	0.087	-0.060	0.001	0.196	-0.644	1.000								
RedoubtR.	0.210	-0.033	-0.157	0.151	0.386	0.441	0.141	-0.325	1.000							
NassR.	0.574	-0.222	0.145	0.565	0.064	0.118	0.565	-0.070	0.496	1.000						
SkeenaR.	0.209	0.051	-0.073	0.006	0.386	0.277	0.028	0.091	-0.147	0.168	1.000					
Birkenhead	-0.018	-0.152	0.130	0.145	0.380	0.594	-0.109	0.374	0.202	-0.002	0.162	1.000				
Early Stuart	-0.295	-0.037	0.024	-0.032	0.210	0.269	-0.077	0.148	0.010	-0.313	0.290	0.527	1.000			
Early Summer	-0.197	0.013	0.011	-0.260	0.253	0.163	-0.071	0.018	0.162	-0.410	0.178	0.323	0.375	1.000		
Late Summer	-0.021	-0.358	-0.229	0.266	0.222	0.488	0.079	-0.001	0.162	0.194	0.124	0.361	0.255	0.397	1.000	
Summer	-0.025	-0.219	0.136	0.139	0.477	0.605	-0.036	0.010	0.293	0.099	0.162	0.493	0.277	0.441	0.462	1

index, with 6 of 6 possible 2-way correlations being positive, and 2 being significant. For stocks within the Prince William Sound area there was a negative correlation (mean correlation = -0.08) in survival rate index. For stocks within the southeast Alaska and northern British Columbia area there was positive correlation (mean correlation = 0.11) in survival rate index, with 22 of the 36 possible 2-way correlations being positive, 6 of which being significant.

Patterns of co-variation in survival rate indices among stocks from different areas were very weak (mean correlation = 0.04) with 223 of 394 possible 2-way correlations being positive and 27 being significantly positive (Table 6).

DISCUSSION

Estimates of commercial catch of sockeye salmon were reasonable surrogates for estimates of total sockeye abundance (i.e. catch plus spawning escapement). This finding is not new - trends in sockeye salmon catches in various management areas have previously been shown to generally mirror abundance time series (e.g. Beamish and Bouillon 1993; Francis and Hare 1994; Hare and Francis 1995). Aggregate sockeye catches are often significant components of abundance time series and therefore the two will be highly correlated.

What is surprising is the similarity in trends of sockeye catches and abundance throughout the North Pacific. Sockeye abundance in Russia and western and central Alaska declined coincident with the 1949 regime shift. Declines also occurred in the eastern North Pacific although they were less severe. Increases in sockeye abundance coincident with the 1977 regime shift were ubiquitous. Other species also benefited from changing ocean conditions after 1977, for example Canadian pink and chum salmon (Irvine and Chen 2004).

Regional abundance patterns associated with the 1989 shift varied. Short-term reductions in sockeye abundance occurred in western and parts of central Alaska but were not evident in Russia or the eastern North Pacific. A lack of a consistent response to the 1989 regime shift for salmon abundance was also reported by Irvine and Chen (2004) and is consistent with Hare and Mantua's (2000) observation that the 1989 regime shift was neither as persuasive as the 1977 regime shift nor a simple return to preceding conditions. Many North American stocks declined in the late 1990s, around the time of the proposed (Peterson and Schwing 2003) 1998 shift, with the most severe declines occurring in southernmost areas.

Body size trends, available for a shorter period (1960–2004) than abundance data, were also consistent among the eight areas in Alaska and British Columbia where these data were available. There were positive 2-way correlations in body sizes among all areas, with a high degree of spatial coherence in the patterns with correlations decreasing with increasing distance. Trends in body size reflected the 1977 and

1989 regime shifts. Body sizes generally increased during regimes of low salmon abundance (1960 – late 1970s, and from the mid 1990s) and decreased during regimes of high salmon abundance (i.e., late 1970s to late 1980s). Ultimate sizes of sockeye salmon are determined during their final period of ocean residence and growth is density-dependent (Rogers 1984). Because many stocks of sockeye salmon have similar marine distributions (Harris 1988; French et al. 1976; Fredin et al. 1977; Habicht et al. 2005), and share their environments with populations of chum and pink salmon (Urawa et al. 2005), temporal patterns in body size probably reflect density-dependent effects caused by the aggregate abundance of salmon in the North Pacific Ocean.

Trends in survival rate indices were similar to trends in catch and abundance. Survival rate changes generally coincided with regime shifts. Survival rate indices prior to the 1949 regime shift (< 1947 BY) averaged much lower than survival indices for the 1949 – 1973 BY. With the exception of the early Stuart, survival rate indices increased for all populations following the 1977 regime shift. Survival rates generally decreased after the 1989 regime shift for stocks in the eastern North Pacific, however many stocks in western and central Alaska showed little change in survival with the 1989 regime shift.

Patterns of co-variation in survival rate indices among the 34 sockeye salmon stocks indicated some coherence at regional scales. Correlations were particularly strong for populations within the Bristol Bay, Chignik, and Fraser river areas. Within-area positive correlations in survivals were much weaker for other areas. There was little positive correlation in survival indices among areas, consistent with the findings of Peterman et al (1998).

We aggregated our data over relatively large areas, appropriate for agencies such as the North Pacific Anadromous Fish Commission and the North Pacific Marine Science Organization. Correlations were generally highest for data from adjacent areas, and decreased with increasing distance. While this illustrated a surprising degree of spatial coherence in sockeye abundances among areas, it also demonstrated that local factors play a role determining regional patterns in salmon survival and abundance.

In Canada, salmon stock assessment and management is becoming increasingly focused on Conservation Units (DFO 2005; Irvine and Riddell 2007), rather than large stock aggregates. Canadian fishery managers need to understand regional differences in productivity; the poor status of some sockeye populations has major effects on the prosecution of fisheries (Irvine et al. 2005). Assessments and forecasts for Canadian sockeye are therefore made for component populations or Conservation Units within major stock groups (e.g. Cass et al. 2006). Because of cyclical abundance patterns, populations that are abundant within an aggregate one year may be uncommon the next year. Population-specific return and escapement estimates are better indices of population status than aggregate catches -- provided they can be con-

trasted with a benchmark. Survival indices allow one to better understand mechanisms responsible for regime shift and climate change effects than abundance, particularly when marine and freshwater mortality can be partitioned.

In contrast, sockeye management and assessment in Alaska and Russia focuses to a greater extent on population aggregations. In these areas, there may be less variability in productivity within aggregates compared to British Columbia. Aggregate catch statistics continue to provide a good indication of stock status in these areas, and presumably will continue to do so provided that exploitation rates do not change dramatically.

It appears that ocean basin-scale environmental processes control the overall production of sockeye salmon, and probably restrict the total production from particular ocean zones. However, local-scale environmental processes can result in regional differences in productivity. Aggregate catch statistics are appropriate indicators of oceanographic conditions over large areas and enable an understanding of the effects of major fisheries, but are not necessarily appropriate indicators of the health of individual populations.

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Appendix 1. Major sockeye salmon stocks for which escapement data (range of years) and escapement-return (brood years) are available. Included are the primary escapement estimation methodology, average catch (thousands, 1995–2004) by area, and average escapement (thousands, 1995–2004), and returns (thousands, 1989–1999 brood years) by stock. E = early; L = late.

Management area	Average catch (thousands) 1995–2004 (percent of North Pacific)	Stocks and component populations	Escapement data			Escapement - return data		
			Escapement method	Years of escapement (range)	Average escapement (thousands) 1995–2004	Brood years (BY) of returns	Average escapement (thousands) BY 89–99	Average returns (thousands) BY 89–99
Russia	5,786 (11%)							
Bristol Bay	20,807 (40%)	Togiak District	Tower	56–04	212	56–99	184	626
		Nushagak District	Tower	56–04	2,380	56–99	2,366	7,108
		Wood	Tower	56–04	1,494			
		Nushagak	Tower/Sonar	56–04	585			
		Igushik	Tower	56–04	305			
		Eastside Districts	Tower	56–04	8,333	56–99	10,557	24,830
		Kvichak	Tower	56–04	3,696			
		Alagnak	Tower	56–04	1,488			
		Naknek	Tower	56–04	1,389			
		Egegik	Tower	56–04	1,177			
		Ugashik	Tower	56–04	927			
Alaska Peninsula	3,761 (7.1%)	Bear R. E. Run	Weir	64–04	337			
		Bear R. L. Run	Weir	64–04	122	80–99	176	580
		Nelson R.	Weir	70–04	265	75–99	241	591
		Ilnik L.	weir	70–04	66			
		Sandy River	Weir	70–04	58			
		Chirstianson L	Aerial	71–04	37			
		Orzinski Lake	Weir	70–04	38			
Chignik	1,477 (2.8%)	Chignik Combined	Weir		754			
		Chignik E. Run	Weir	22–04	447	22–99	461	1,391
		Chignik L. Run	Weir	22–04	307	22–99	345	1,113
Kodiak	3,526 (6.8%)	Pauls Bay	Weir	78–04	27			
		Afognak Lake	Weir	78–04	64			
		Akalura Lake	Weir	23–04	17			
		Saltery Lake	Weir	76–04	43			
		Ayakulik R.	Weir	29–04	282	65–99	384	674
		Upper Station E. Run	Weir	69–04	53	69–99	43	127
		Upper Station L. Run	Weir	66–04	183	70–99	211	469
		Frazer L.	Weir	66–04	177	66–99	218	543
		Karluk Combined	Sonar	22–04	777	22–99	796	1,449
		Karluk E. Run	Weir	22–04	332	80–99		
		Karluk L. Run	Weir	22–04	445	80–99		

Appendix 1 (continued).

Management area	Average catch (thousands) 1995–2004 (percent of North Pacific)	Stocks and component populations	Escapement data			Escapement - return data		
			Escapement method	Years of escapement (range)	Average escapement (thousands) 1995–2004	Brood years (BY) of returns	Average escapement (thousands) BY 89–99	Average returns (thousands) BY 89–99
Cook Inlet	3,271 (6.2%)	Kenai R. L. Run	Sonar	78–04	886	68–99	688	2,910
		Russian R. E. Run	Weir	65–04	47	65–97	35	87
		Kasilof R.	Sonar	75–04	303	75–98	197	761
		Yentna R	Sonar	81–04	114			
		Fish Cr.	Weir	38–04	55			
		Crescent R.	Sonar	75–04	70	75–98	63	93
Prince William Sound	2,302 (4.4%)	Eshamy R.	Weir	61–04	29	65–00		
		Cognill R.	Weir	62–04	39	69–00	26	112
		Copper R.	Sonar	78–04	798	65–97	706	2,213
Southeast Alaska - N. British Columbia	3,671 (7%)	Situk R.	Weir	76–04	54	76–97	64	118
		Lost R.	Aerial	72–04	3			
		Italio R.	Aerial	73–04	3	72–97	4	4
		Klukshu R.	Weir	76–04	15	76–96	17	17
		East Alsek R.	Aerial	72–04	36	72–97	55	89
		Chilkat R.	Weir	76–04	171	76–95	128	296
		Chilkoot R.	Weir	76–04	50	76–95	55	43
		Redoubt L.	Weir	82–04	37	82–96	35	33
		Taku R.	Mark/Recap	84–04	103			
		Tahltan L.	Weir	79–04	25			
		Mainstem Stikine R.	Visual	79–04	32			
		McDonald Lake	Aerial	82–04	58			
		Aggregate N. BC (nuSEDs)		48–04	1,522			
		Nass River	Mark/Recap	82–04	247	82–98	304	967
		Skeena River	Mark/Recap	70–02	1,271	70–00	1,179	3,158
		Other N. BC (nuSEDs)	Various	50–04	186			
S. British Columbia - Washington	2,175 (4.1)	Aggregate S. BC (nuSEDs)		48–04	3,493			
		Fraser R aggregate (nuSEDs)	Various	48–04	3,134			
		Birkenhead	Visual	48–04	100	48–99	134	299
		Birkenhead	Visual	48–04				
		Big Silver	Visual	73–04				
		Early Stuart (Takla, Middle R., Trembleur)	Visual/Carcass census	48–04	84	48–99	176	387

Appendix 1 (continued).

Management area	Average catch (thousands) 1995–2004 (percent of North Pacific)	Stocks and component populations	Escapement data			Escapement - return data		
			Escapement method	Years of escapement (range)	Average escapement (thousands) 1995–2004	Brood years (BY) of returns	Average escapement (thousands) BY 89–99	Average returns (thousands) BY 89–99
		Early Summers		48–04	262	48–99	193	574
		Chilliwack	Visual	74–04				
		Nahatlatch	Visual	72–04				
		Upper Pitt	Mark/Recap	48–04				
		Gates	CarcassCensus	48–04				
		Upper Adams	Visual	74-04				
		Anstey	Visual	74–04				
		Cayenne	Visual	73–04 (not continuous)				
		Eagle	Visual	73–04				
		Scotch	CarcassCensus	48–04				
		Seymour	Visual	48–04				
		Fennell	Visual	54–04				
		Raft	Visual	48–04				
		Taseko	Visual	75–04				
		Nadina	Visual/Carcass Weir	48–04				
		Bowron	Visual	48–04				
		Summers	Various	48–02	1,917	48–99	1,981	6,425
		Chilko	Mark/Recap	48–04				
		Mitchell		49–04				
		Horsefly	CarcassCensus	48–04				
		McKinley	Visual	53–04				
		Quesnel	Visual	61–04 (not continuous)				
		Stellako	Weir	48–04				
		Late Stuart	Visual/Carcass Census	48–04				
		Late Summers (lates)	Various	48–04	374	48–99	860	2,390
		Cultus	Weir	24–04				
		Widgeon	Visual	95–04				
		Harrison	Visual	48–04				
		Weaver	Visual/Carcass Census	48–04				
		Portage	Visual	49–04				574

Appendix 1 (continued).

Management area	Average catch (thousands) 1995–2004 (percent of North Pacific)	Stocks (bold) and component populations	Escapement data			Escapement - return data		
			Escapement method	Years of escapement (range)	Average escapement (thousands) 1995–2004	Brood years (BY) of returns	Average escapement (thousands) BY 89–99	Average returns (thousands) BY 89–99
		Lwr Shuswap	Weir	49–04				
		Mid Shuswap	Visual	74–04				
		S. Thomson	Visual	72–04				
		Other S. BC (nuSEDs)	Various	48–04	303		303	
		L. Washington	Lock Count	72–04	430		247	

Chinook Salmon – Trends in Abundance and Biological Characteristics

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Abstract: Chinook salmon, *Oncorhynchus tshawytscha*, the least abundant but largest in size of the five major Pacific salmon species, are widely distributed throughout the North Pacific Rim. Although precise numbers spawning in many rivers are little known, many stocks have only a small percentage of their historic abundance levels, and more than 50 stocks have become extinct. Over the past decade commercial catches have fluctuated between one and two million fish annually with an additional 0.6–0.9 million fish caught in recreational, subsistence, and aboriginal fisheries. About half of all commercial catches are made in the United States, particularly in Alaska and Pacific-Northwest states, with the remainder caught, in descending order, by Canada, Russia, and Japan. Within the U. S., nine fish populations are listed in Pacific-Northwest states as threatened or endangered, according to the Endangered Species Act (ESA). While no formal ESA-type listings occur in other areas, some populations in Canada and Russia are of special concern due to declining trends. Current trends in abundance are reviewed from different regions with a focus on stocks of concern but also including some stocks whose trends are relatively stable. While equivocal in improving the status of many depressed wild stocks, hatcheries are important in helping maintain fisheries and general abundance in some areas. Chinook salmon are characterized by high plasticity and life-history variability, as seen in their multiple age groups, diverse temporal migration behavior as they return to natal streams, distinct races with separate freshwater and ocean life-history behavior patterns, and red-fleshed and white-fleshed forms. Long-term declines in the average size and age of Chinook salmon appear to be continuing for some stocks and fisheries. The species may be establishing new populations and expanding its range into higher latitudes, possibly due to global warming and other climatic changes.

Keywords: Chinook salmon abundance, biological characteristics, hatcheries, range extension, reduced size and age

INTRODUCTION

Chinook salmon, *Oncorhynchus tshawtscha*, indigenous to the Pacific coast of North America and Asia are among the least abundant salmon populations but achieve the largest adult size of all Pacific salmon. The species is widely distributed with important spawning stocks ranging from central California in North America to the Bering Straits and southward along the Asian coast to the Amur River (Major et al. 1978). North of the Bering Straits, smaller runs occur in Alaska's Kotzebue Sound and possibly eastward into the Beaufort Sea along the north coast of Alaska and northern Canada (McPhail and Lindsey 1970; Hart 1973; McLeod and O'Neal 1983). While it is known that Chinook salmon range widely throughout the Sea of Okhotsk, the Bering Sea, and northern portions of the North Pacific Ocean (Healey 1991), the southern limits of their oceanic distributions are more

fragmented and less well known. Along the North American coast a few Chinook salmon have been recovered south of 40°N Latitude, including two coded, wire-tagged (CWT) fish caught by a groundfish fishery (see CWT database at http://www.rmis.org/cwt/cwt_qbe.html). Others have been captured by recreational fisheries off San Diego, California (Miller and Lea 1972) and Baja California, Mexico (Cruz-Aguero 1999).

Throughout their range, Chinook salmon show a wide diversity of life-history characteristics, including run-timing, variable ages of juvenile seaward migration and different oceanic behavior patterns. Maturing adults can enter natal streams over an extended period from February to December and are commonly referred to as winter, spring, summer, or fall runs. After emerging from natal gravels, juvenile Chinook salmon that are reared in fresh water but migrate to sea after only a few months are referred to as ocean-type salmon,

whereas those that are reared in fresh water for one to two years before migrating to sea are referred to as stream-type salmon. These two life-history types also exhibit distinctly different oceanic migration patterns (Healey 1983; Hartt and Dell 1986).

Significant commercial fisheries for Chinook salmon are found along the North American coast near California, Oregon, Washington, British Columbia, and in southeastern Alaska, central Alaska, and Bristol Bay. Substantial freshwater fisheries may also occur in many rivers, including the Sacramento, Klamath, Columbia, Fraser, Skeena, Nass, Kuskokwim, Yukon, Kamchatka, and Bolshaya rivers.

In North America, a Pacific Salmon Treaty (PST) established in 1985 between the United States and Canada and amended in 1999 (http://www.psc.org/pubs/Treaty.pdf) plays a significant role in regulating fisheries for Chinook salmon from the mid-Oregon coast northward to the southeast of Alaska (Shepard and Argue 2005). The treaty, administered by the Pacific Salmon Commission (PSC), facilitated major rebuilding programs for depressed stocks through careful management and restricted harvest levels in many fisheries. The bilateral Chinook Technical Committee (CTC) oversees scientific assessments of stock status and establishes management protocols for Chinook salmon fisheries within areas of PSC jurisdiction.

Besides influencing commercial fisheries, Chinook salmon are important in many recreational, subsistence, and aboriginal fisheries throughout much of its range. The species is highly prized in both freshwater and marine sport fisheries due, in part, to its large size and relative scarcity compared to other salmon. Sport fisheries for Chinook salmon play an important role in tourism development in many areas and positively impact local economies. In rural areas and among native and aboriginal peoples, Chinook salmon have historically played a vital role in subsistence and ceremonies. From 2003 to 2004, the harvest of Chinook salmon in North American recreational, subsistence, and aboriginal fisheries exceeded 900 thousand fish (Table 1). The catch for PST-regulated fisheries in areas of the Pacific Northwest is documented in Anon. (2005b) for the years 1975–2004.

The role of hatcheries has been important to the history and legacy of Chinook salmon over the past century, especially in North America. For much of this history, Chinook salmon hatcheries were considered to be an acceptable means of mitigating many of the deleterious, anthropogenic causes of habitat loss, declining fishery catches, and depressed populations. In more recent times, however, hatcheries are seen not as an unequivocal solution to these issues, but as part of the problem.

For long periods of time, hatcheries were not adequately monitored or evaluated to measure their intended effects, and more recent scientific information has shown that past hatchery practices exacerbated many issues they were intended to solve (Anon. 1996a; Levin et al. 2001).

Although hatcheries remain controversial in many scientific circles, most hatchery programs now have implemented important changes in past practices and operate under more clearly defined objectives: to help rebuild depressed natural runs or to stabilize fisheries. Several Chinook salmon fisheries in North America are now only possible because of hatchery programs. In some rivers, hatchery fish comprise a majority of the fish population. For example, by 1987, hatchery-originating Chinook salmon dominated adult returns to the Columbia River, comprising 70% of the spring run, 80% of the summer run, and over 50% of the fall run (Anon. 1996a).

From the 1993 to 2001 brood years, between 250 and 298 million juvenile Chinook salmon were released annually from North American hatcheries. The state of Washington has the largest program, releasing up to 160 million juvenile Chinook salmon per year, followed by Canada, Oregon, California, Alaska, and Idaho (Table 2). Chinook salmon hatcheries in Russia occur on a much smaller scale. The Malkinski Hatchery in the lower reaches of the Bolshaya River currently is the nation's only hatchery for Chinook salmon. Annual releases from Malkinsky Hatchery, 1983–2004, ranged from 0.3–1.2 million juveniles (excluding 1989, a year of high mortalities in the hatchery).

In this report, we will consider current trends in abundance of certain stocks of Chinook salmon from around the Pacific Rim. Our focus will be on major stocks and stock groups that represent significant components of the species in different regions. This focus will include stocks at risk due to declining populations, and stocks that may be in danger of extinction, as well as some stocks that show stable or improving population tendencies. We focus on escapements of adults into natal spawning areas whenever possible, however, where escapement data is limited or unavailable, we use terminal fishery harvest data, although harvest data alone may not accurately reflect stock status.

The intent of this review is to provide a snapshot of current trends in the abundance of Chinook salmon throughout its Pacific range and also to review some of the unique biological characteristics of the species.

Table 1. Recent North American harvest of Chinook salmon by recreational, subsistence, and aboriginal fisheries (in thousands of fish).

Area	Recreational	Subsistence-aboriginal	Total
WOC[1]	371	NA	
BC[2]	193	18	
AK[3]	193	167[4]	
Totals	757	185	942

[1]Washington, Oregon, and California data from Bartlett (2005).
[2]British Columbia data from Irvine et al. (2005).
[3]Alaska data from Eggers (2005) and from Anon. (2005a) Subsistence Report.
[4]Subsistence-aboriginal data from Alaska are from 2003, all other data from 2004.

Table 2. Numbers of juvenile Chinook salmon released from brood years 1993–2001 by Washington, Oregon, California, Idaho, Alaska, and British Columbia (BC)/Yukon (in millions of fish)[1].

	1993	1994	1995	1996	1997	1998	1999	2000	2001
Washington	146.5	156.9	147.9	154.8	146.5	129.6	133.4	122.1	133.3
BC/Yukon	51.3	54.7	46.3	59.5	50.5	55.6	59.2	49.5	54.6
Oregon	49.9	45.3	40.3	30.8	30.5	28.2	23.5	25.1	27.9
California	29.1	33.4	38.9	32.6	47.7	33.4	28.9	33.4	29.3
Idaho	10.2	0.8	0.8	3.6	8.8	7.8	3.7	11.4	11.9
Alaska	8.5	6.4	8.3	8.1	7.9	8.7	8.8	8.6	8.6

[1]Data from Pacific States Marine Fish Commission RMIS Database.

TRENDS IN ABUNDANCE

Precise data on present numbers of Chinook salmon spawning in many rivers is not known, however, many populations were historically more numerous than they are today—particularly those populations in the U. S. Pacific Northwest. A long list of factors contributing to these declines includes major losses of spawning and juvenile rearing habitats due to logging, urbanization, and other developmental practices; over-fishing; water allocations for argricultural, mineralogical , urban, and other uses; and the presence of dams that block or compromise upstream and downstream migration patterns in addition to flooding spawning and rearing habitats.

Harvest data gleaned from the Food and Agriculture Organization of the United Nations (FAO) for different countries around the Pacific Rim indicate that catches of Chinook salmon averaging around 25,000 mt in 1950 had declined to about half that level by 2004 (Fig. 1). By 1950, many major runs of Chinook salmon had already diminished significantly in size from levels observed in the first half of the century (Mundy 1997; Lichatowich 1999). Over the past decade, Pacific Rim commercial catches of Chinook salmon have generally fluctuated between one and two million fish annually with over half of the catch coming from the U.S. and the remainder coming, in descending order, from Canada, Russia, and Japan. The U.S commercial catch is almost evenly divided between Alaska and Pacific Northwest states. Sharp declines in the Canadian commercial harvest in the mid 1990s were driven by conservation concerns for domestic salmon stocks, and were not reflective of corresponding declines in overall Canadian Chinook salmon abundance.

Washington-Oregon-Idaho-California (WOIC)

Trends in salmon abundance along North America's western coast have been the subject of several studies in recent years. In a detailed review of salmon stocks in Pacific Northwest states, Nehlsen et al. (1991) found that over 50 native stocks of Chinook salmon from Washington, Oregon, Idaho, California, Nevada, and British Columbia had

become extinct. Most extinct British Columbian stocks were located above the Grand Coulee Dam (completed in 1941), which blocked runs into the upper reaches of the Columbia River Drainage.

The U.S Endangered Species Act (ESA) of 1973 has had a major impact on Chinook salmon management and conservation in the Pacific Northwest. During the 1980s, as it became more evident that many salmon stocks in the region were in various stages of decline and several were on the verge of extinction, scientists began exploring how ESA could be applied to threatened stocks of salmon. In response to petitions that called for various salmon populations to be listed under ESA, the National Marine Fisheries Service (NMFS) initiated coast-wide status reviews by Biological Review Teams (BRT) for each species (Kope and Wainwright 1998). Following principles developed in a series of policy decisions, NMFS determined that a salmon population or group of populations would be considered a distinct ESA listing if it represented an evolutionary significant unit (ESU) of the species (Waples 1991). By this definition, nine ESUs of Chinook salmon were ultimately listed as either threatened or endangered (Anon. 1996b). These listings included three ESUs from California, five from the Columbia River Basin, and one from Puget Sound (Table 3). Geographic drainages for some of these ESU groups have overlapping ranges (Fig. 2).

The first Chinook salmon population was listed under ESA in 1990 after the Sacramento River winter run past the Red Bluff Diversion Dam reached a record low count of 550 adults in 1989 (Nehlsen et al. 1991). The initial listing as "threatened" for this ESU was upgraded to "endangered" in 1994 (Table 3). Following the implementation of a recovery plan that includes fishery closures and hatchery fish supplementation the Sacramento River winter run Chinook salmon (Fig. 3) has begun to show modest improvements (Anon. 2004a; Killam 2005).

The Klamath River Drainage in northern California and southern Oregon historically had both spring and fall runs of Chinook salmon. Spring runs in this system now do not occur due to a series of hydro-dams and other factors (Hamilton et al. 2005). Fall run Chinook salmon in the Klamath
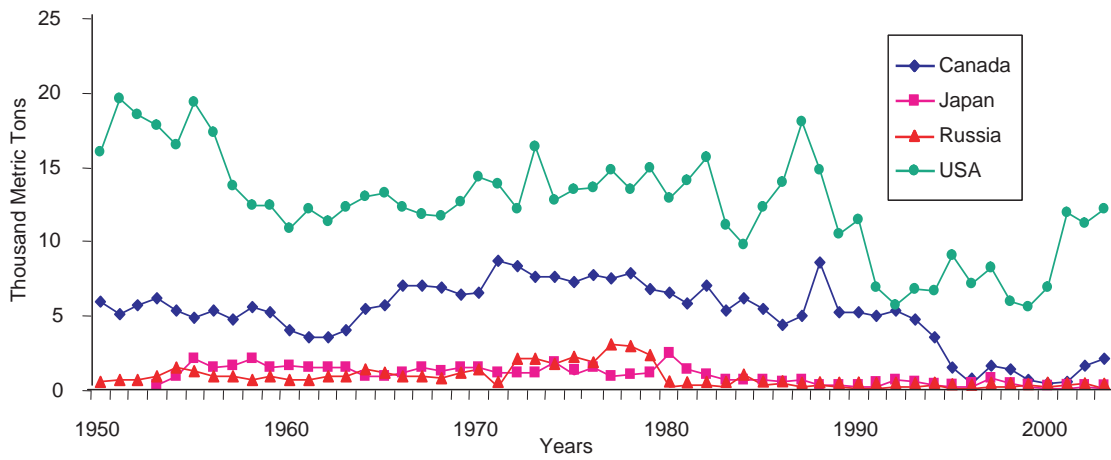
Fig. 1. Commercial harvest of Chinook salmon in metric tonnes by Canada, Japan, Russia, and United States, 1950–2003. Data from FAO.
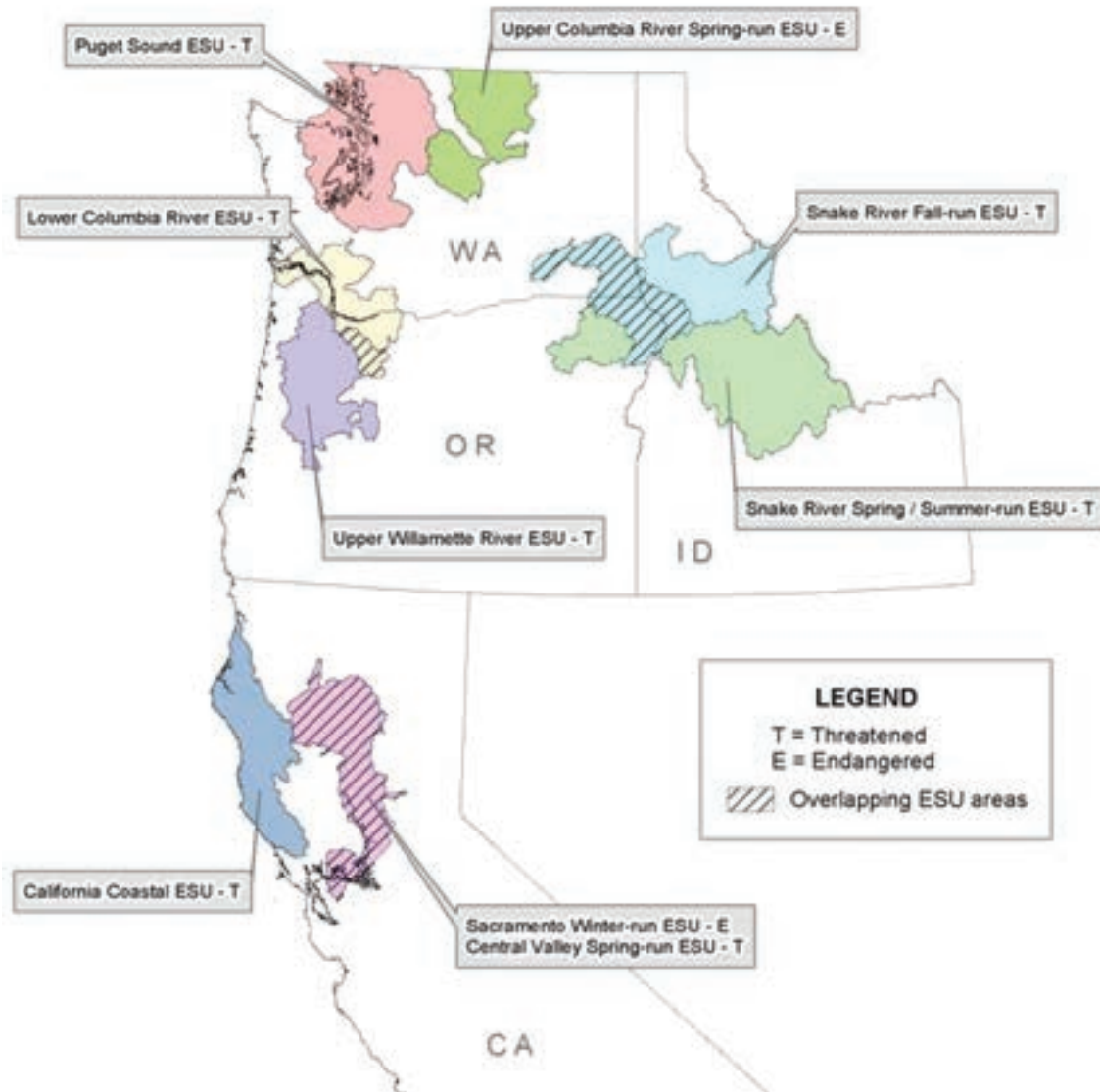

Fig. 2. Geographic drainages of nine Chinook salmon ESUs in the states of Washington, Oregon, Idaho, and California listed either as threatened or endangered under the U. S. Endangered Species Act of 1974. Map by Barbara Seekins, NOAA Fisheries.

Table 3. Threatened and endangered Chinook salmon in the Pacific Northwest listed under the Endangered Species Act (ESA) of the United States.

ESU[1] groups	Year endangered[2]	Year threatened[3]
Sacramento River Winter- Run ESU	1994	1990
California Central Valley Spring- Run ESU		1999
California Coastal ESU		1999
Lower Columbia River ESU		1999
Upper Wilamette River ESU		1999
Upper Columbia River Spring- Run ESU	1999	
Snake River Spring/Summer- Run ESU		1992
Snake River Fall-Run ESU		1992
Puget Sound ESU		1999

[1]ESU or evolutionary significant unit is defined by NMFS as a population that:
    a) is substantially reproductively isolated from conspecific populations, and
    b) represents an important component in the evolutionary legacy of the species.
[2]Endangered means ESU is in danger of extinction.
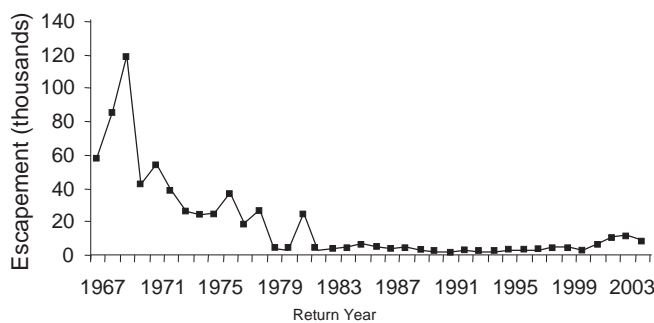[3]Threatened means ESU is likely to become endangered.

Fig. 3. Sacramento River Winter-Run Chinook salmon escapements, 1967–2004. Data from Calif. Dept. Fish Game.
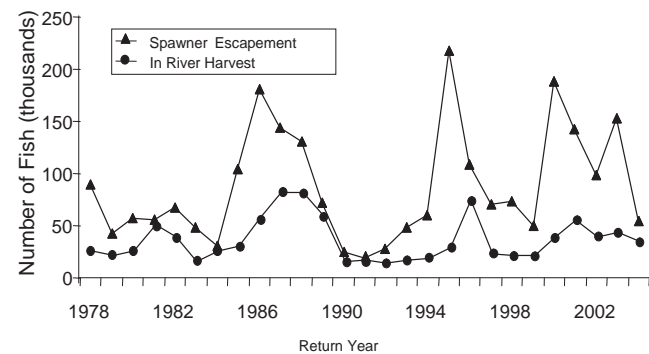

Fig. 4. Escapement and in-river harvest of Klamath River Fall-Run Chinook salmon, 1978–2004. Data from U.S. Fish and Wildlife Service.

Fig. 5. Counts of Spring-, Summer-, and Fall-Run Columbia River Chinook salmon adults past Bonneville Dam, 1977–2005. Data from Columbia River Data Access in Real Time (DART) system (http://www.cbr.washington.edu/dart/adult.html).

River system was not listed under ESA by the BRT, however; this ESU is of concern because of its fluctuations and frequently low escapements. Current runs of Chinook salmon into the Klamath River drainage system are characterized by significant recreational and subsistence fisheries on the river (Fig. 4).
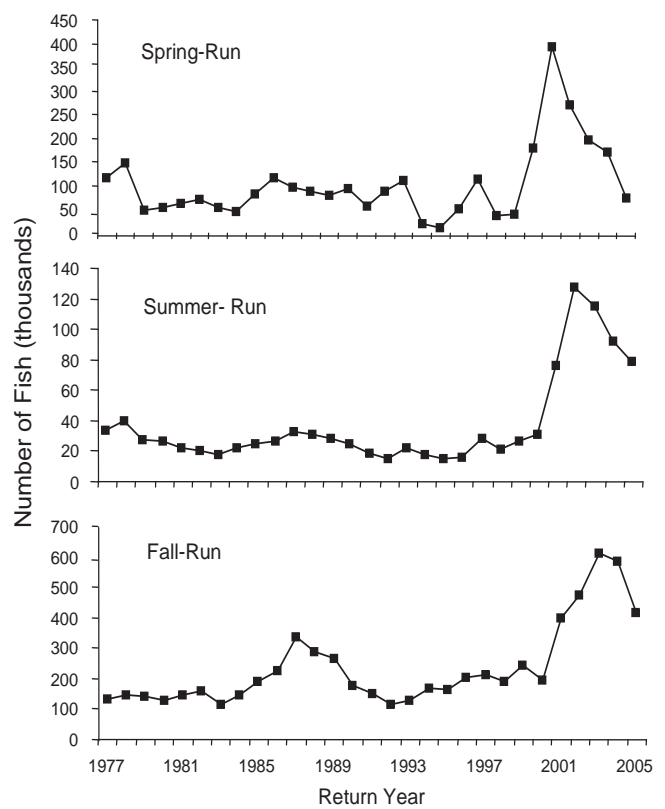
There are over 40 dams in the Columbia River Basin, and the first dam encountered by salmon returning from their ocean migration is Bonneville at river kilometer (Rkm) 235. Daily counts of upstream-migrating salmon and other anadromous fishes passing through this dam provide the
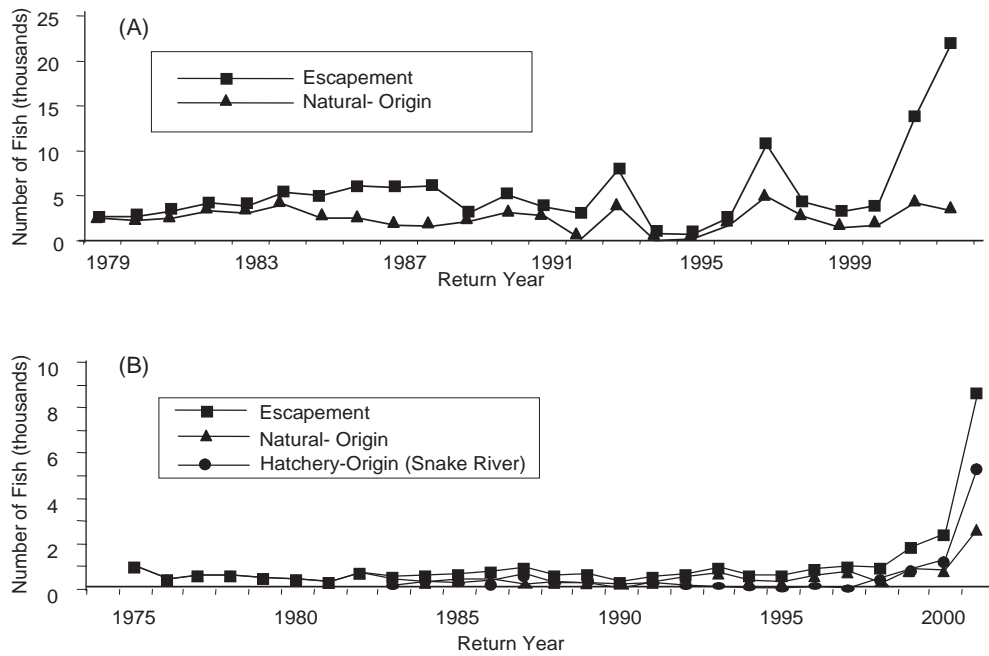
Fig. 6. Escapements of Snake River Chinook salmon past Lower Granite Dam: (A) total escapement and natural origin escapement of Summer-Run, 1979–2002; (B) total escapement, natural origin escapement, and Snake River hatchery origin Fall-Run, 1975–2001. Data from Anonymous (2003a, Figs. A.2.1.1 and A.2.2.2).
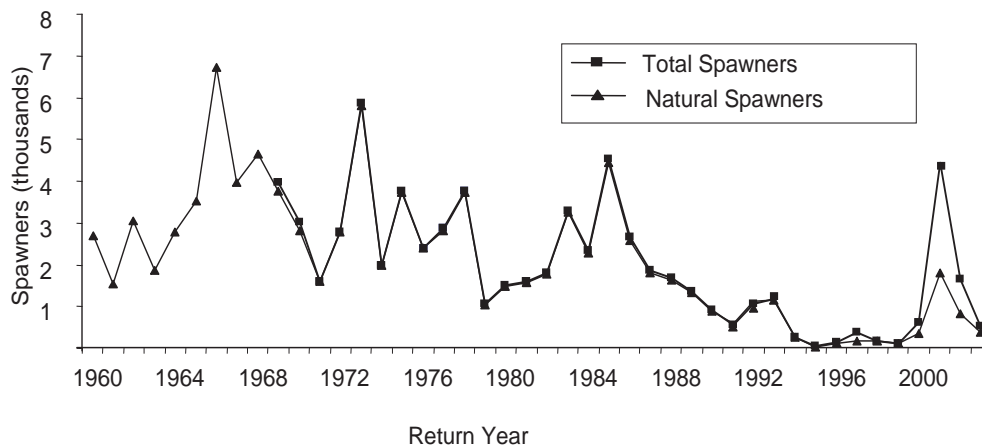

Fig. 7. Estimated number of Chinook salmon spawners in the Wenatchee River, a key indicator stock for the Upper Columbia River Spring-Run ESU, 1960–2003. Data from Anonymous (2003a, Fig. A.2.3.1).

number of each species returning to the river each year. Chinook salmon counts at Bonneville Dam are maintained under the DART system (http://www.cbr.washington.edu/dart/adult.html) in a temporal mode representing run-timing of spring-, summer-, and fall-run fish. Bonneville Dam counts of Chinook salmon are usually designated "spring run fish" from March through May, "summer run fish" from June through July, and "fall run fish" from August through November. Chinook salmon counts at Bonneville Dam from 1977–2005 show a significant increase in returns beginning in 2000 and 2001. However, more recently counts have begun to decline, especially for spring- and summer-run fish (Fig. 5).

The Lower Granite Dam, located on a major tributary of the Columbia River at Snake River Rkm 173, is the last major dam salmon pass before reaching the remaining available spawning grounds in the Snake River Basin. Counts of Chinook salmon at this dam provide assessments on the status of two ESA-listed groups: Snake River spring/summer-run and Snake River fall-run ESUs. Counts of Chinook salmon passing the Lower Granite Dam are evaluated by BRT groups to determine what portion of total escapement is comprised of hatchery salmon and and what portion of natural-origin salmon (Anon. 2003a). The principle of "natural origin" includes both wild salmon and naturally spawning salmon

that may have some measure of hatchery parentage. The distinction between hatchery- and natural-origin salmon is drawn because ESA seeks to foster rebuilding programs with naturally spawning fish and, where possible, to minimize the influence of hatcheries. Snake River summer-run Chinook salmon escapements past the Lower Granite Dam illustrate the differences between total escapement and natural-origin fish (Fig. 6A). When monitoring the Snake Rive fall-run escapement, one of the more contentious Columbia Basin listings, BRT assessors track an additional level of escapement by distinguishing hatchery-origin fish from Snake River stocks (Fig. 6B). Unfortunately, current BRT assessments past the Lower Granite Dam do not include Snake River stock calculations for the most recent years (2003–2005).

Wenatchee River Chinook salmon represent one of the last vestiges of the large Upper Columbia River spring run ESU that was all but totally extirpated with the completion of the Grand Coulee Dam in 1941. BRT estimates of Chinook salmon spawning in the Wenatchee River show a long, steady decline that, even with hatchery supplementation, now includes only a few hundred natural-origin fish (Fig. 7).

British Columbia–Yukon

In a review of Chinook salmon in British Columbia and the Yukon Territory, Slaney et al. (1996) identified from a total of 866 stocks 17 stocks as extinct and 60 others at high or moderate risk of extinction. Slaney's stocks at risk included, among others, some populations near West Vancouver Island, the Strait of Georgia, and certain Fraser River stocks. Concern over declines in population remains today. Canada currently has a two-step system for listing stocks at risk of extinction. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is a committee comprised of representatives from government, academia and other non-governmental organizations, which assesses the risk of a species' extinction. It can then recommend that the federal government place the endangered species under the legal protection of the Species at Risk Act (SARA). If the recommendation is accepted, COSEWIC formulates a recovery plan. COSEWIC's determinations of stock status are somewhat different from those definitions used by Slaney et al. (1996). Presently, there are no Chinook salmon stocks listed under SARA in Canada. Henderson and Graham (1998) attributed overall increases in spawning escapements of Chinook salmon in British Columbia in the late 1980s and 1990s to implementation of the Pacific Salmon Treaty as well as other actions taken in Canada to address domestic conservation concerns. This general increase in abundance has continued since the new regulations were implemented.

Fortunately, the Fraser River, unlike the Columbia River, has no main-stem dams to impede migration of salmon stocks throughout the basin. Like Columbia River salmon, Fraser River Chinook salmon cycle through as spring-, sum-
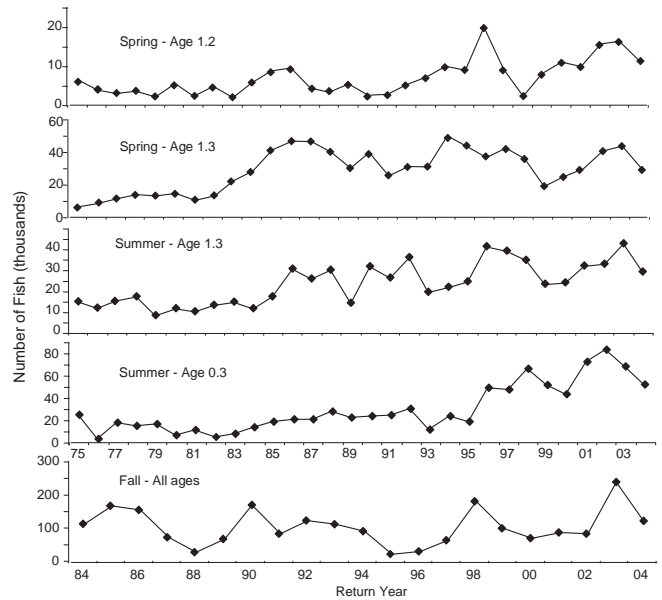

Fig. 8. Escapements of Fraser River Chinook salmon, Spring- and Summer-Run by life-history type,1975–2004, and Fall-Run, 1984–2004 (Anonymous 2005b).
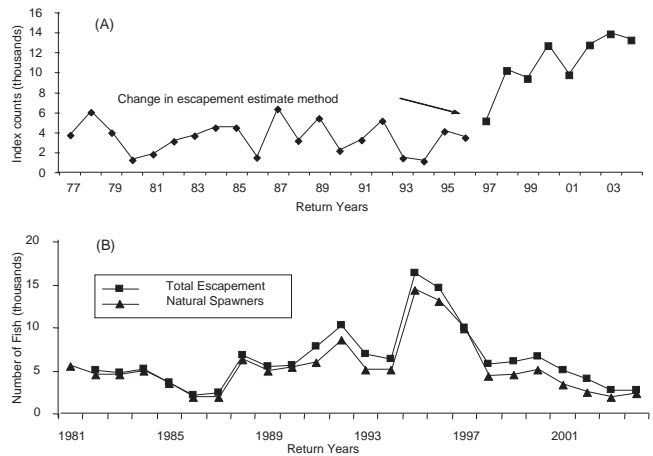

Fig. 9. Escapements of Fall-Run Chinook salmon in the Strait of Georgia: (A) an index of escapements for a group of stocks in the upper strait, 1977–2004; (B) escapement in the Cowichan River in the lower strait, 1981–2004 (Anonymous 2005b).

mer- and fall-run types. As in the Columbia River, each of these runs is comprised of many individual stocks that exist at different levels of stability or decline. Ocean age .2 and age .3 spring-run Chinook salmon escapements of stream-type spawners in the Fraser River show similar escapement trends but exhibit different levels of abundance, whereas ocean age .3 summer-run fish from both stream and ocean-type spawners show similar escapement trends and similar abundance levels (Fig. 8). Both spring-run and summer-run Chinook salmon show a decline in escapements from recent highs in the Fraser River. Fall-runs have demonstrated considerable year-to-year fluctuation (between 100 and 200 thousand fish)
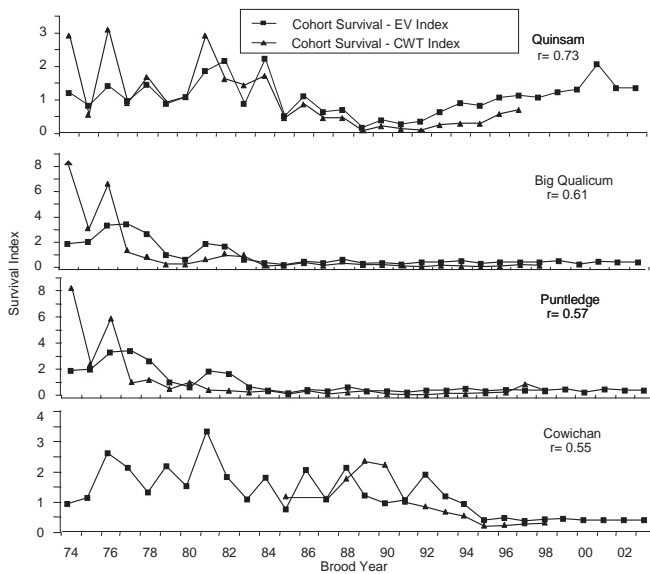
Fig. 11. Escapement index counts of Chinook salmon for 14 West Vancouver Island streams, 1993–2004 (Anonymous 2005b).

Fig. 10. Chinook salmon EV and CWT cohort survival indices for Strait of Georgia hatcheries, 1974–2003, including Quinsam Hatchery in the upper strait and Big Qualicum, Puntledge, and Cowichan Hatcheries in the lower strait. EV indices are scalers generated by the PSC coastwide Chinook salmon model which reflect annual variability in natural mortality in the initial year of ocean residence while CWT indices represent survival of CWT-marked releases to age two. Standardized EV scalers are plotted for complete and incomplete broods, while only completed brood values are plotted for CWT survivals; the r value is the correlation coefficient between the two indices, which indicates that the two generally track one another. Data from CTC files.

with no clear long-term trend (Fig. 8). The Harrison River stock, which comprises the vast majority of this stock group, represents one of the largest single Chinook salmon stocks in the Pacific Northwest.

Perhaps the most recent conservation concern in Canada is Chinook salmon in the Strait of Georgia. While CTC assessments indicate low abundance levels throughout the Strait of Georgia, there are discernable regional differences between the Upper Georgia Strait (UGS; relatively higher) and the Lower Georgia Strait (LGS; relatively lower), in population trends, and in survival rates (Anon. 2003b, 2004b). Generally difficult to enumerate, the UGS group consists largely of stocks heavily influenced by glacial runoff. While there is evidence that the UGS group has increased in abundance since the late 1990s, this observation may be confounded by a concurrent change in enumeration methodology for this stock group (Fig. 9A). The LGS stock group, however, has undergone continuous declines over the past decade. The stock group's status is primarily monitored via returns to the Cowichan River, which has traditionally been the largest single stock within the stock group. The Cowichan River is monitored for total escapement and natural spawners, because hatchery-origin fish may also spawn in the river. Escapements to the Cowichan have declined precipitously since the mid-1990s (Fig. 9B).
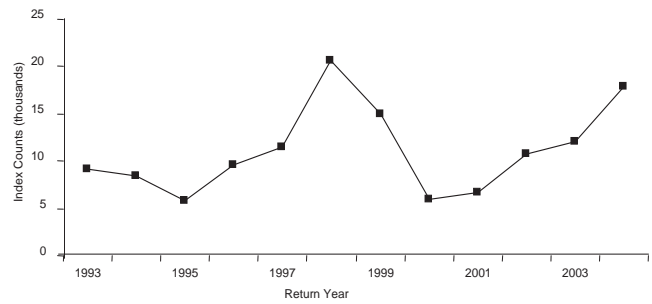
A difference in the status of Chinook salmon in UGS and LGS is also apparent in the survival trends of hatchery smolts released in the two regions. The survival rate for smolts released at Quinsam Hatchery in UGS is measured by coded wire tag (CWT) recoveries and an environmental variable (EV) scaler index generated by the PSC coast-wide model (Anon. 2004c); these measurements indicate an improving survival trend since the early 1990s (Fig. 10). In contrast, survival rates among three LGS hatchery stocks (Big Qualicum, Puntledge, and Cowichan) show considerable decline for both CWT and EV indices—in some cases, since the early 1980s—and have remained at these low levels ever since (Fig. 10). These comparisons illustrate a puzzling difference in the status of Chinook salmon in the two regions of the Strait of Georgia. Possible factors that could be contributing to the present condition include: overfishing by commercial and recreational fisheries, changes in the environment (Beamish et al. 2004), shifts in abundance, changes in predators' and competitors' behavior (Beamish and Neville 2000; Beamish et al. 2003), and differences in migration patterns.

One possible difference in survival patterns in the UGS and LGS areas could be the amount of time juvenile and immature Chinook salmon spend in the Strait of Georgia. According to Healey (1980) numerous juvenile, ocean-type Chinook salmon remain in the LGS throughout much of their first ocean year, and, judging from sport fishery catches, juveniles remain plentiful in the LGS during their second ocean year (Argue et al. 1983). However, CWT recovery information indicates that the majority of these fish are from the LGS. Furthermore, based on CWT recoveries of Quinsam-hatchery Chinook salmon, UGS stocks, unlike LGS stocks, are far-north-migrating and are generally intercepted outside the Georgia Strait, suggesting that some deleterious factors within the Strait of Georgia have led to population declines in the lower Strait of Georgia.

Beamish and Neville (2000) identified spiny dogfish and river lampreys as major predators of juvenile Chinook salmon in the Strait of Georgia. They estimated that 1.4 million spiny dogfish ate the equivalent of all 7.7 million juvenile Chinook and coho salmon released from local hatcheries
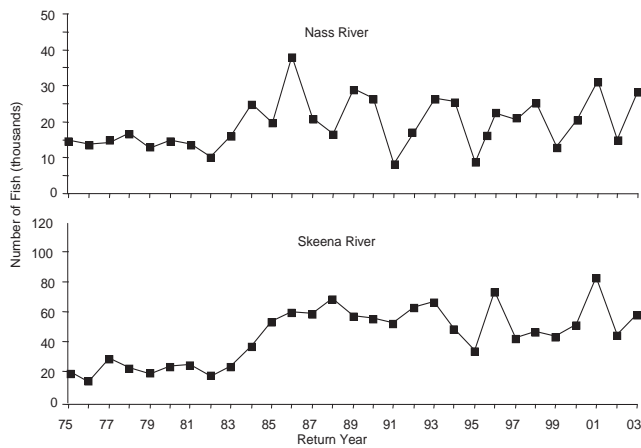
Fig. 12. Chinook salmon escapements for the Skeena and Nass rivers in northern British Columbia, 1975–2003 (Anonymous 2005b).

Fig. 13. Chinook salmon escapements for the Taku and Stikine rivers in southeastern Alaska, 1975–2003 (Anonymous 2005b).

Fig. 14. Chinook salmon escapements for the Kenai River in south-central Alaska, 1986–2004. Data from ADF&G Sport Fish Division.

in 1988, and that 3.0 to 3.9 million river lampreys killed 20 million and 18 million juvenile Chinook salmon in 1990 and 1991, respectively (Beamish and Neville 2000). Ford and Ellis (2005) found that fish-eating killer whales residing in the Strait of Georgia have a strong preference for Chinook salmon throughout much of the year, especially in the LGS. Ford and Ellis (2005) suggested that this preference for Chinook salmon could influence the year-round distribution patterns of resident killer whales within the Strait of Georgia. Selective predation is only one factor that may cause differences in the survival rates of LGS and UGS Chinook salmon stocks.

Another Chinook salmon stock group of conservation concern in British Columbia is found on the west coast of Vancouver Island. This group consists of several dozen small, coastal fall-run populations. A 14-stream index is used to monitor the abundance of this stock group (Anon. 2003b; 2004b). While this index shows modest increases in the last four years (Fig. 11), these populations are still of concern because several individual stocks in the group remain at very low levels.

In general, the abundance of Chinook salmon stocks in central and northern British Columbia has been relatively stable. This stability is illustrated by Nass and Skeena river returns, the two largest stock aggregates in northern British Columbia. While returns to the Nass have remained stable, those to the Skeena have improved since the signing of the PST (Fig. 12).

Alaska

In contrast to declining trends in Chinook salmon's abundance in WOIC and some areas in British Columbia, most salmon populations throughout Alaska are stable. Baker et al. (1996) identified 63 spawning aggregates of Chinook salmon in southeastern Alaska and, of the 31 groups with sufficient data for evaluation, they found only one that exhibited a de-
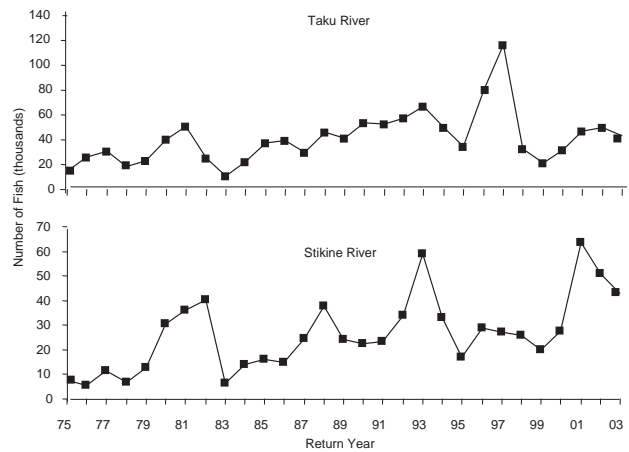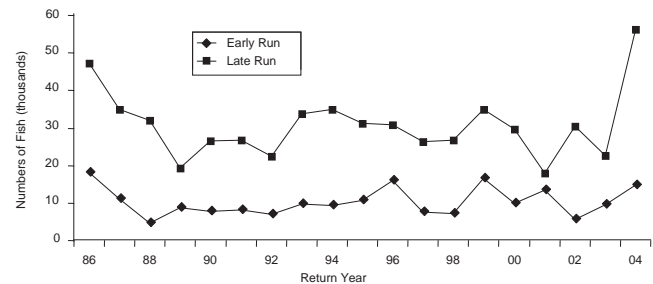
clining escapement trend. Burger and Wertheimer (1995) and Wertheimer (1997) found that commercial harvests of Alaskan Chinook salmon have remained relatively stable over time when compared to harvests of other species. In southeastern Alaska, the Chinook salmon fishery is dominated by commercial trolling, and a large portion of the harvest in the region originates from more southerly, non-Alaska stocks. Harvesting of the region's Chinook salmon is regulated by catch limits and treaty oversight. Although Chinook salmon are the first to return to Alaska's rivers each year, commercial fisheries are normally allowed to target only those fish in terminal areas of a few river systems (Heard and Anderson 1999). After a lengthy period of fishery closures and stock rebuilding under PSC oversight, limited commercial gill-net fisheries were allowed in 2005 to target Chinook salmon returning to the Stikine and Taku rivers.

Escapement trends for stock groups in two of southeastern Alaska's largest drainages (Taku and Stikine rivers) show relatively stable patterns (Fig. 13). These trans-boundary rivers originate either in British Columbia or the Yukon Territory and fall under PSC oversight. In the Cook Inlet region of south-central Alaska, Kenai River Chinook salmon that support a major in-river sport fishery participate in early and late runs, spawning in upper and lower portions of the
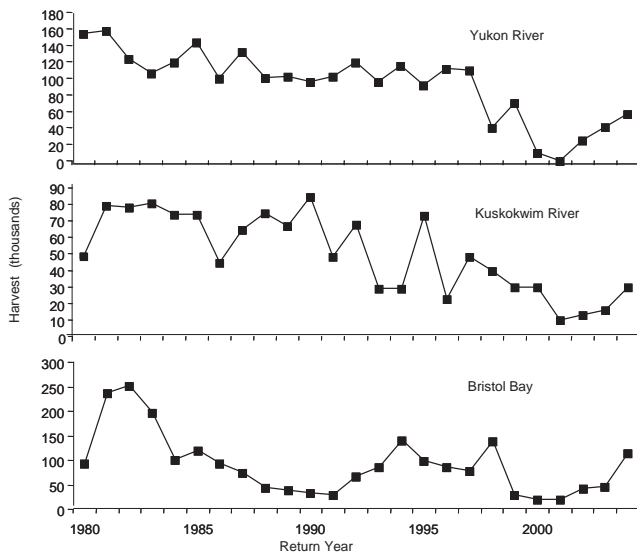
Fig. 15. Chinook harvest from Bristol Bay and from the Kuskokwim and Yukon rivers in western Alaska, 1980–2004. Data from ADF&G Commercial Fish Division.

Fig. 16. Chinook salmon harvest from the Kamchatka Peninsula in Russia, 1934–2005: (A) total harvest; (B) harvest from east and west Kamchatka. Data from SakhNIRO.

drainage. Escapements to both run segments show relatively stable trends (Fig. 14).

Western Alaska represents the region in Alaska where there is most concern over trends in abundance of Chinook salmon. Long-term data sets on escapements in this region are somewhat spotty, therefore, harvest data are used to assess trends, although these data may not reflect true abundance trends. Harvest data from Bristol Bay, and the Kuskokwim and Yukon rivers all suggest declining abundance (Fig. 15). Although overall harvests in Bristol Bay show a downward trend, the commercial fishery mainly targets Nushugak River stocks that are still thought to be relatively healthy. Declining catches in both the Kuskokwim and Yukon rivers is a matter for concern for rural Alaskans living in these regions. Chinook salmon runs into the Yukon River, another trans-boundary river originating in Canada and managed under a separate treaty annex, were so low in 2001 that no commercial fishery was allowed. One area of concern regarding the present status of stocks in the Kuskokwim and Yukon rivers is the Chinook salmon by-catch made from these systems by groundfish trawl fisheries in the Bering Sea.

Russia

On the Asian side of the Pacific Rim, harvest data are also used to look at trends in abundance because precise escapement data is limited. Radchenko (1998) reviewed abundance trends in Russian Chinook salmon and reported that commercial catches had declined from a peak of 3,000 mt in the 1970s to 600 mt in the late 1990s. Commercial catches declined further to 200 mt by 2003 but have begun rebounding in the last two years to their current levels above 500 mt (Fig. 16). Although Chinook salmon fisheries are found on
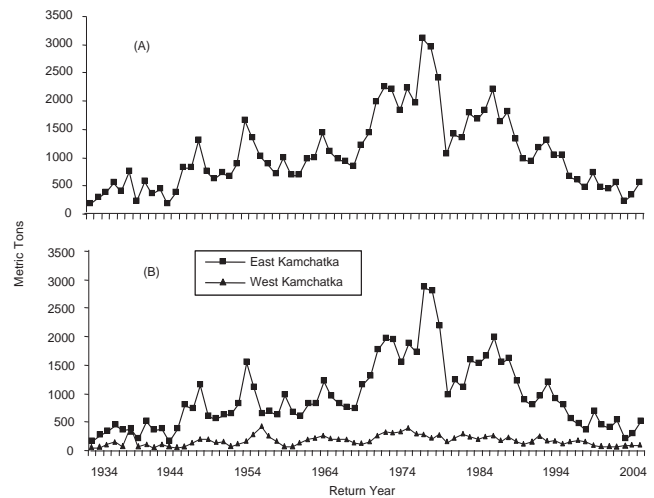
both the east and west coast of the Kamchatka Peninsula, 80–90% of Russia's total catch comes from eastern Kamchatka, and primarily from the Kamchatka River, whereas catches from western Kamchatka are mostly from the Bolshaya River. Radchenko (1998) suggested that there were several small, unexploited stocks in western Kamchatka that could increase the commercial catch up to 100 mt if exploited. In recent years, the total run—catch plus escapement—of Chinook salmon off both the east and west coasts of the Kamchatka Peninsula has been estimated by Shevlyakov to be at 170–190 thousand fish annually. Only in a few smaller rivers (Koly, Pymta, and Kikhchik) have adult escapements been at favorable levels in recent years. The major river systems (Kamchatka and Bolshaya) appear to have had inadequate escapements over the past decade due to intense fishing and increased in-river poaching.

The run timing of Chinook salmon returning to spawn in Russian rivers follows a late spring/summer-run pattern. In the Kamchatka River the commercial fishery begins operating shortly after the ice breaks up in May, and its operation peaks in June (Vronskiy 1972). Chinook salmon in the Kamchatka River also migrate in early and late runs. Some early-run fish may enter the river in spring before the ice is out. The run timing of the early run extends from late May to mid-June with spawning occurring from mid-June through August and peaking in late July to early August. Run timing of the late run extends from early July to late August with spawning occurring from mid-August to mid-September and peak spawning occurring in late August. Stream-type Chinook salmon are typical of populations in Asia although some under-yearling juveniles do migrate to sea from Kamchatka Peninsula rivers. However, adult returns for such stocks are extremely poor.

BIOLOGICAL CHARACTERISTICS

Chinook salmon are an extremely plastic species with the most diversified and complex life history among Pacific salmon. The species has many unique biological characteristics including highly evolved and diversified run timing (Waples et al. 2004) with adults entering rivers and spawning in almost every month of the year, exhibiting stream-type and ocean-type life-history forms with different freshwater and oceanic migration behavior patterns (Healey 1983), and some having both red- and white-fleshed forms (Godfrey 1975; Hard et al. 1989).

The coastal region of northern British Columbia and southeastern Alaska (54°–56°N) represents a transition area where populations with ocean-type life histories generally predominate to the south whereas stream-type life histories predominate to the north (Healey 1983). Upriver populations from longer trans-boundary rivers that penetrate the coastal mountain range in southeastern Alaska exhibit stream-type life histories in fresh water. These populations also display more extensive oceanic migration patterns characteristic of stream-type biology. Other populations of Chinook salmon from shorter rivers restricted to the coastal regions of southeastern Alaska also exhibit stream-type life history in fresh water (i.e. yearling smolts). In contrast, however, while at sea these coastal populations tend to exhibit an ocean-type life-history behavior by foregoing distant open oceanic migrations and instead remaining in coastal waters. Such transitional behavior in fresh water and marine life histories could result from a predisposition for ocean-type life history based on genetic origin modified by environmental constraints requiring extended freshwater rearing at higher latitudes. Guthrie and Wilmot (2004) speculated that cooler northern climates could cause this type of a life-history shift. Gharrett et al. (1987) suggested that, based on the intermediate genetic composition of Chinook salmon populations, the salmon in the region could have come from two different refuges in their post-glacial colonization. Based on current life-history behavior patterns, it seems likely that under such a scenario, coastal populations seaward of the coastal mountain range in southeastern Alaska arose from ancestral ocean-type parents, while longer-migrating, upriver populations (i.e. in the Taku, Stikine, and Alsek rivers) arose from stream-type parentage.

An important life-history characteristic in Chinook salmon is long-term change in size and age. Ricker (1980) pointed out that Chinook salmon had decreased in average size by 50% or more during the twentieth century. Potential contributing causes include the selective effects of fisheries, changes in oceanic environments, habitat loss, dams such as the Grand Coulee that eliminated entire runs of large fish, and the prevalence of contemporary hatchery production in many areas. According to Ricker (1980, 1981), fisheries—especially troll fisheries—which capture both immature and maturing fish, ultimately bring about a decrease in propor-

tions of older, larger fish in spawning populations and an increase in younger, smaller fish. Ricker believes that declines resulted from a progressive deterioration of the genetic basis for maturation at older ages. A somewhat-related process may also be underway when hatchery-produced fish return at a reduced size per age and earlier in run-timing in comparison with naturally spawned fish. Increased maturation timing in hatchery fish is partly due to accelerated growth of juveniles in the hatchery environment (Larson et al. 2004). In some supplementation programs, however, hatchery males and females are returning not only earlier but also at smaller sizes than naturally-spawned fish in both Chinook salmon (Anon. 2004a; Pearsons et al. 2004), and in steelhead (Mackey et al. 2001).

In a later study Ricker (1995) noted that, by the early 1990s, declines in size of Chinook salmon catches (particularly 1951 through 1975) had been fully reversed or at least arrested in many but not all areas. Dramatic reversals were

Fig. 17. Average weights of Chinook salmon caught in regional Alaska fisheries, 1994-2004. AAH is average annual harvest in thousands of fish for each region. R^2 values measure how well the regression line fits data in the trend line. Data from ADF&G Commercial Fish Division.

Fig. 18. Average weights of the 30 largest Chinook salmon caught in a May sport fishing derby near Juneau, Alaska, 1998–2005. R^2 measures how well the regression line fits data in the trend line. Data from Tlingit-Haida Central Council.

Fig. 19. Composition of Kamchatka River Chinook salmon by life-history types, 1958–2004. Data from KamchatNIRO.

Fig. 20. Average weight of Kamchatka River Chinook salmon spawners by decade, 1958–2004. Data from KamchatNIRO.

evident in Canadian troll catches in Areas 1 and 5, but less so in Area 12. Dominated by troll fisheries, all Chinook salmon gear catches in southeastern Alaska showed similar improvements in size, whereas all gear catches in Puget Sound showed only minor improvement. Ricker expressed puzzlement over possible causes of these size reversals in certain areas. He indicated that changes in fishing regulations and minimum size limits are of special importance for troll fisheries since many Chinook salmon are caught while still growing rapidly, and he suggested that the factor or factors responsible for the size reversal might be apparent if age composition data were available (Ricker 1995).
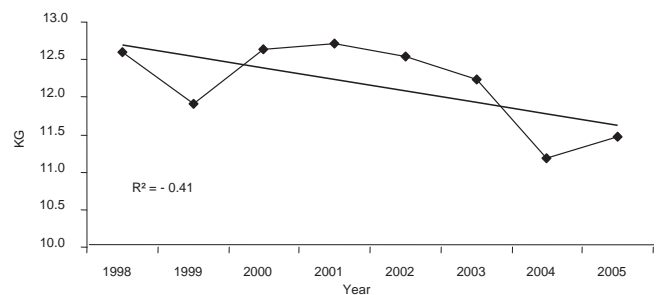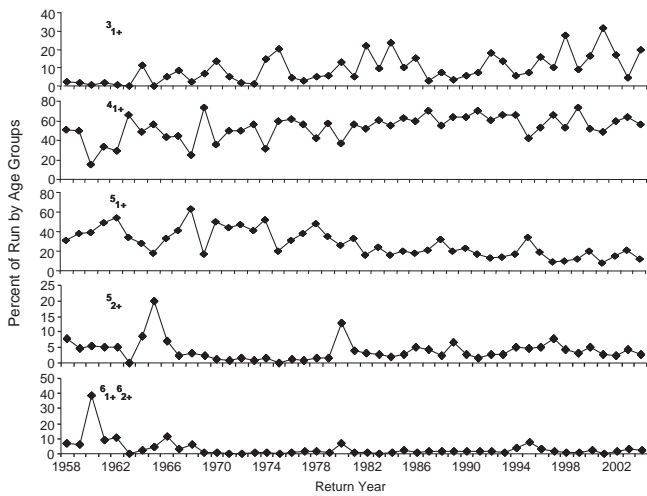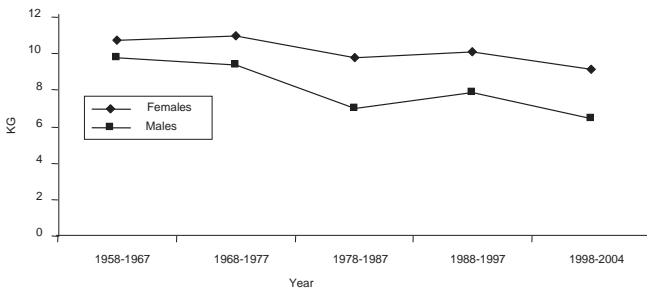
Bigler et al. (1996) found that seven of nine individual or aggregate populations of Chinook salmon between 1975 and 1993 had decreased in average size. The increase in average size observed by two commercial troll fisheries in California and British Columbia may have been the result of changes in fishery regulations (e.g. size limits were increased in British Columbia's troll fisheries in 1987). The average weights of Chinook salmon in several Alaskan commercial fisheries from 1994 to 2004 continue to show declines (Fig. 17). A recreational fishery for Chinook salmon in the vicin-

ity of Juneau, Alaska, primarily targets returning Taku River spawners during the month of May. The average size of the largest 30 fish caught from 1998 to 2005 show a declining trend (Fig. 18). From 1958 to 2004, the percentage of older Chinook salmon in the Kamchatka River has decreased while the percentage of younger fish has increased (Fig. 19). These dramatic changes in age structure are accompanied by modest decreases in the average size of returning fish, a trend that is more pronounced in males than females (Fig. 20).

CONCLUSIONS

The present population of Chinook salmon stocks from around the Pacific Rim varies considerably according to different geographic regions. For example, in the U.S. Pacific Northwest states of Washington, Oregon, Idaho, and California, where nine stock groups are currently listed by the ESA as threatened or endangered species, many wild stocks remain at or near record low levels. Other stocks in this area are already extinct due to a long list of contributing factors, including over-fishing; loss of spawning and rearing habitats; impediments to upstream or downstream migration due to river dams; watershed logging; water allocations for farming, mining and navigation; and generalized industrialization and urbanization throughout the region. Over time, recovery programs for some ESA-listed stock groups in the Sacramento and Columbia rivers are beginning to cause minor improvements.

While no Chinook salmon stocks are legally protected under the Canadian COSEWIC and SARA programs, some stocks in southern British Columbia, especially in the Lower Strait of Georgia and West Vancouver Island, are of special concern. The status of stocks in central and northern British Columbia are either stable or improving, due, in part, to conservation measures implemented since the PST was signed in 1985.

Chinook salmon stocks throughout most of Alaska are comparatively stable with the exception of stocks in the Kuskowim and Yukon rivers in the western part of the state. The by-catch of these stocks in Bering Sea groundfish trawl fisheries is an issue of concern. Stocks in the southeastern portion of Alaska have also benefited from PST conservation and managerial oversight.

As reflected by harvest trends, Russian stocks of Chinook salmon on the Kamchatka Peninsula have declined from 3000 mt in the 1970s to around 500 mt currently. Russia's two major river systems (Kamchatka and Bolshaya) appear to have had serious declines in escapement size over the past two decades due to intense fishing and in-river poaching.

Historically, hatcheries have played significant, and often controversial, roles in many Chinook salmon issues—especially in the U.S. Pacific Northwest and southern British Columbia. The use of hatcheries to mitigate anthropogenic-caused declines in wild stocks is now viewed as counterproductive to the long-term health and genetic diversity of

salmon species. Nevertheless, many hatcheries today are implementing important changes in past practices and operate under more clearly defined objectives to help rebuild depressed wild runs or to help support certain fisheries. Hatcheries continue to play a major role in many important Chinook salmon populations and fisheries.

The selective harvesting of both immature and older, larger Chinook salmon in various fisheries, habitat loss, the extirpation of certain stocks of large fish, variable growth conditions in marine environments, some hatchery practices, and long-term environmental changes may all be interacting to cause significant long-term reductions in the average size and age of Chinook salmon .

Given the complex life history and plasticity exhibited by Chinook salmon, it is not surprising that this species may be responding to warming climatic conditions in Arctic environments by expanding its range into new regions, especially into the Beaufort Sea drainages of North America. Previous accounts of collections have been reported for the Mackenzie River (Mcleod and O'Neil 1983) and the Coppermine River (Hart 1973) in the Canadian Arctic. Other recent developments suggest that the species is also becoming more prevalent in Arctic regions of Alaska. These developments include recent catches of 20–25 adult Chinook salmon annually by subsistence fisheries in Elson Lagoon near Point Barrow (C. George, Dept. of Wildlife Mgmt., North Slope Borough, P.O. Box 69 Barrow, AK 99723, pers. comm.) and the collection of four adult Chinook in Ublutuoch River, a tributary stream near the mouth of the Coville River, AK, in 2004 (Moulton 2005).

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Chinook Salmon – Trends in Abundance and Biological Characteristics

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Abstract: Chinook salmon, *Oncorhynchus tshawytscha*, the least abundant but largest in size of the five major Pacific salmon species, are widely distributed throughout the North Pacific Rim. Although precise numbers spawning in many rivers are little known, many stocks have only a small percentage of their historic abundance levels, and more than 50 stocks have become extinct. Over the past decade commercial catches have fluctuated between one and two million fish annually with an additional 0.6–0.9 million fish caught in recreational, subsistence, and aboriginal fisheries. About half of all commercial catches are made in the United States, particularly in Alaska and Pacific-Northwest states, with the remainder caught, in descending order, by Canada, Russia, and Japan. Within the U. S., nine fish populations are listed in Pacific-Northwest states as threatened or endangered, according to the Endangered Species Act (ESA). While no formal ESA-type listings occur in other areas, some populations in Canada and Russia are of special concern due to declining trends. Current trends in abundance are reviewed from different regions with a focus on stocks of concern but also including some stocks whose trends are relatively stable. While equivocal in improving the status of many depressed wild stocks, hatcheries are important in helping maintain fisheries and general abundance in some areas. Chinook salmon are characterized by high plasticity and life-history variability, as seen in their multiple age groups, diverse temporal migration behavior as they return to natal streams, distinct races with separate freshwater and ocean life-history behavior patterns, and red-fleshed and white-fleshed forms. Long-term declines in the average size and age of Chinook salmon appear to be continuing for some stocks and fisheries. The species may be establishing new populations and expanding its range into higher latitudes, possibly due to global warming and other climatic changes.

Keywords: Chinook salmon abundance, biological characteristics, hatcheries, range extension, reduced size and age

INTRODUCTION

Chinook salmon, *Oncorhynchus tshawtscha*, indigenous to the Pacific coast of North America and Asia are among the least abundant salmon populations but achieve the largest adult size of all Pacific salmon. The species is widely distributed with important spawning stocks ranging from central California in North America to the Bering Straits and southward along the Asian coast to the Amur River (Major et al. 1978). North of the Bering Straits, smaller runs occur in Alaska's Kotzebue Sound and possibly eastward into the Beaufort Sea along the north coast of Alaska and northern Canada (McPhail and Lindsey 1970; Hart 1973; McLeod and O'Neal 1983). While it is known that Chinook salmon range widely throughout the Sea of Okhotsk, the Bering Sea, and northern portions of the North Pacific Ocean (Healey 1991), the southern limits of their oceanic distributions are more fragmented and less well known. Along the North American coast a few Chinook salmon have been recovered south of 40°N Latitude, including two coded, wire-tagged (CWT) fish caught by a groundfish fishery (see CWT database at http://www.rmis.org/cwt/cwt_qbe.html). Others have been captured by recreational fisheries off San Diego, California (Miller and Lea 1972) and Baja California, Mexico (Cruz-Aguero 1999).

Throughout their range, Chinook salmon show a wide diversity of life-history characteristics, including run-timing, variable ages of juvenile seaward migration and different oceanic behavior patterns. Maturing adults can enter natal streams over an extended period from February to December and are commonly referred to as winter, spring, summer, or fall runs. After emerging from natal gravels, juvenile Chinook salmon that are reared in fresh water but migrate to sea after only a few months are referred to as ocean-type salmon,

whereas those that are reared in fresh water for one to two years before migrating to sea are referred to as stream-type salmon. These two life-history types also exhibit distinctly different oceanic migration patterns (Healey 1983; Hartt and Dell 1986).

Significant commercial fisheries for Chinook salmon are found along the North American coast near California, Oregon, Washington, British Columbia, and in southeastern Alaska, central Alaska, and Bristol Bay. Substantial freshwater fisheries may also occur in many rivers, including the Sacramento, Klamath, Columbia, Fraser, Skeena, Nass, Kuskokwim, Yukon, Kamchatka, and Bolshaya rivers.

In North America, a Pacific Salmon Treaty (PST) established in 1985 between the United States and Canada and amended in 1999 (http://www.psc.org/pubs/Treaty.pdf) plays a significant role in regulating fisheries for Chinook salmon from the mid-Oregon coast northward to the southeast of Alaska (Shepard and Argue 2005). The treaty, administered by the Pacific Salmon Commission (PSC), facilitated major rebuilding programs for depressed stocks through careful management and restricted harvest levels in many fisheries. The bilateral Chinook Technical Committee (CTC) oversees scientific assessments of stock status and establishes management protocols for Chinook salmon fisheries within areas of PSC jurisdiction.

Besides influencing commercial fisheries, Chinook salmon are important in many recreational, subsistence, and aboriginal fisheries throughout much of its range. The species is highly prized in both freshwater and marine sport fisheries due, in part, to its large size and relative scarcity compared to other salmon. Sport fisheries for Chinook salmon play an important role in tourism development in many areas and positively impact local economies. In rural areas and among native and aboriginal peoples, Chinook salmon have historically played a vital role in subsistence and ceremonies. From 2003 to 2004, the harvest of Chinook salmon in North American recreational, subsistence, and aboriginal fisheries exceeded 900 thousand fish (Table 1). The catch for PST-regulated fisheries in areas of the Pacific Northwest is documented in Anon. (2005b) for the years 1975–2004.

The role of hatcheries has been important to the history and legacy of Chinook salmon over the past century, especially in North America. For much of this history, Chinook salmon hatcheries were considered to be an acceptable means of mitigating many of the deleterious, anthropogenic causes of habitat loss, declining fishery catches, and depressed populations. In more recent times, however, hatcheries are seen not as an unequivocal solution to these issues, but as part of the problem.

For long periods of time, hatcheries were not adequately monitored or evaluated to measure their intended effects, and more recent scientific information has shown that past hatchery practices exacerbated many issues they were intended to solve (Anon. 1996a; Levin et al. 2001).

Although hatcheries remain controversial in many scientific circles, most hatchery programs now have implemented important changes in past practices and operate under more clearly defined objectives: to help rebuild depressed natural runs or to stabilize fisheries. Several Chinook salmon fisheries in North America are now only possible because of hatchery programs. In some rivers, hatchery fish comprise a majority of the fish population. For example, by 1987, hatchery-originating Chinook salmon dominated adult returns to the Columbia River, comprising 70% of the spring run, 80% of the summer run, and over 50% of the fall run (Anon. 1996a).

From the 1993 to 2001 brood years, between 250 and 298 million juvenile Chinook salmon were released annually from North American hatcheries. The state of Washington has the largest program, releasing up to 160 million juvenile Chinook salmon per year, followed by Canada, Oregon, California, Alaska, and Idaho (Table 2). Chinook salmon hatcheries in Russia occur on a much smaller scale. The Malkinski Hatchery in the lower reaches of the Bolshaya River currently is the nation's only hatchery for Chinook salmon. Annual releases from Malkinsky Hatchery, 1983–2004, ranged from 0.3–1.2 million juveniles (excluding 1989, a year of high mortalities in the hatchery).

In this report, we will consider current trends in abundance of certain stocks of Chinook salmon from around the Pacific Rim. Our focus will be on major stocks and stock groups that represent significant components of the species in different regions. This focus will include stocks at risk due to declining populations, and stocks that may be in danger of extinction, as well as some stocks that show stable or improving population tendencies. We focus on escapements of adults into natal spawning areas whenever possible, however, where escapement data is limited or unavailable, we use terminal fishery harvest data, although harvest data alone may not accurately reflect stock status.

The intent of this review is to provide a snapshot of current trends in the abundance of Chinook salmon throughout its Pacific range and also to review some of the unique biological characteristics of the species.

Table 1. Recent North American harvest of Chinook salmon by recreational, subsistence, and aboriginal fisheries (in thousands of fish).

Area	Recreational	Subsistence-aboriginal	Total
WOC[1]	371	NA	
BC[2]	193	18	
AK[3]	193	167[4]	
Totals	757	185	942

[1]Washington, Oregon, and California data from Bartlett (2005).
[2]British Columbia data from Irvine et al. (2005).
[3]Alaska data from Eggers (2005) and from Anon. (2005a) Subsistence Report.
[4]Subsistence-aboriginal data from Alaska are from 2003, all other data from 2004.

Table 2. Numbers of juvenile Chinook salmon released from brood years 1993–2001 by Washington, Oregon, California, Idaho, Alaska, and British Columbia (BC)/Yukon (in millions of fish)[1].

	1993	1994	1995	1996	1997	1998	1999	2000	2001
Washington	146.5	156.9	147.9	154.8	146.5	129.6	133.4	122.1	133.3
BC/Yukon	51.3	54.7	46.3	59.5	50.5	55.6	59.2	49.5	54.6
Oregon	49.9	45.3	40.3	30.8	30.5	28.2	23.5	25.1	27.9
California	29.1	33.4	38.9	32.6	47.7	33.4	28.9	33.4	29.3
Idaho	10.2	0.8	0.8	3.6	8.8	7.8	3.7	11.4	11.9
Alaska	8.5	6.4	8.3	8.1	7.9	8.7	8.8	8.6	8.6

[1]Data from Pacific States Marine Fish Commission RMIS Database.

TRENDS IN ABUNDANCE

Precise data on present numbers of Chinook salmon spawning in many rivers is not known, however, many populations were historically more numerous than they are today—particularly those populations in the U. S. Pacific Northwest. A long list of factors contributing to these declines includes major losses of spawning and juvenile rearing habitats due to logging, urbanization, and other developmental practices; over-fishing; water allocations for argricultural, mineralogical , urban, and other uses; and the presence of dams that block or compromise upstream and downstream migration patterns in addition to flooding spawning and rearing habitats.

Harvest data gleaned from the Food and Agriculture Organization of the United Nations (FAO) for different countries around the Pacific Rim indicate that catches of Chinook salmon averaging around 25,000 mt in 1950 had declined to about half that level by 2004 (Fig. 1). By 1950, many major runs of Chinook salmon had already diminished significantly in size from levels observed in the first half of the century (Mundy 1997; Lichatowich 1999). Over the past decade, Pacific Rim commercial catches of Chinook salmon have generally fluctuated between one and two million fish annually with over half of the catch coming from the U.S. and the remainder coming, in descending order, from Canada, Russia, and Japan. The U.S commercial catch is almost evenly divided between Alaska and Pacific Northwest states. Sharp declines in the Canadian commercial harvest in the mid 1990s were driven by conservation concerns for domestic salmon stocks, and were not reflective of corresponding declines in overall Canadian Chinook salmon abundance.

Washington-Oregon-Idaho-California (WOIC)

Trends in salmon abundance along North America's western coast have been the subject of several studies in recent years. In a detailed review of salmon stocks in Pacific Northwest states, Nehlsen et al. (1991) found that over 50 native stocks of Chinook salmon from Washington, Oregon, Idaho, California, Nevada, and British Columbia had become extinct. Most extinct British Columbian stocks were located above the Grand Coulee Dam (completed in 1941), which blocked runs into the upper reaches of the Columbia River Drainage.

The U.S Endangered Species Act (ESA) of 1973 has had a major impact on Chinook salmon management and conservation in the Pacific Northwest. During the 1980s, as it became more evident that many salmon stocks in the region were in various stages of decline and several were on the verge of extinction, scientists began exploring how ESA could be applied to threatened stocks of salmon. In response to petitions that called for various salmon populations to be listed under ESA, the National Marine Fisheries Service (NMFS) initiated coast-wide status reviews by Biological Review Teams (BRT) for each species (Kope and Wainwright 1998). Following principles developed in a series of policy decisions, NMFS determined that a salmon population or group of populations would be considered a distinct ESA listing if it represented an evolutionary significant unit (ESU) of the species (Waples 1991). By this definition, nine ESUs of Chinook salmon were ultimately listed as either threatened or endangered (Anon. 1996b). These listings included three ESUs from California, five from the Columbia River Basin, and one from Puget Sound (Table 3). Geographic drainages for some of these ESU groups have overlapping ranges (Fig. 2).

The first Chinook salmon population was listed under ESA in 1990 after the Sacramento River winter run past the Red Bluff Diversion Dam reached a record low count of 550 adults in 1989 (Nehlsen et al. 1991). The initial listing as "threatened" for this ESU was upgraded to "endangered" in 1994 (Table 3). Following the implementation of a recovery plan that includes fishery closures and hatchery fish supplementation the Sacramento River winter run Chinook salmon (Fig. 3) has begun to show modest improvements (Anon. 2004a; Killam 2005).

The Klamath River Drainage in northern California and southern Oregon historically had both spring and fall runs of Chinook salmon. Spring runs in this system now do not occur due to a series of hydro-dams and other factors (Hamilton et al. 2005). Fall run Chinook salmon in the Klamath
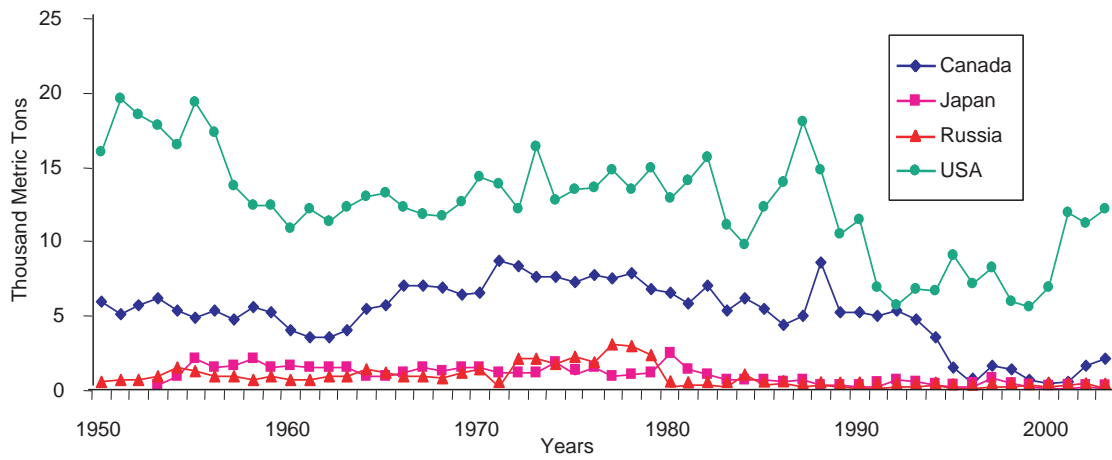
Fig. 1. Commercial harvest of Chinook salmon in metric tonnes by Canada, Japan, Russia, and United States, 1950–2003. Data from FAO.
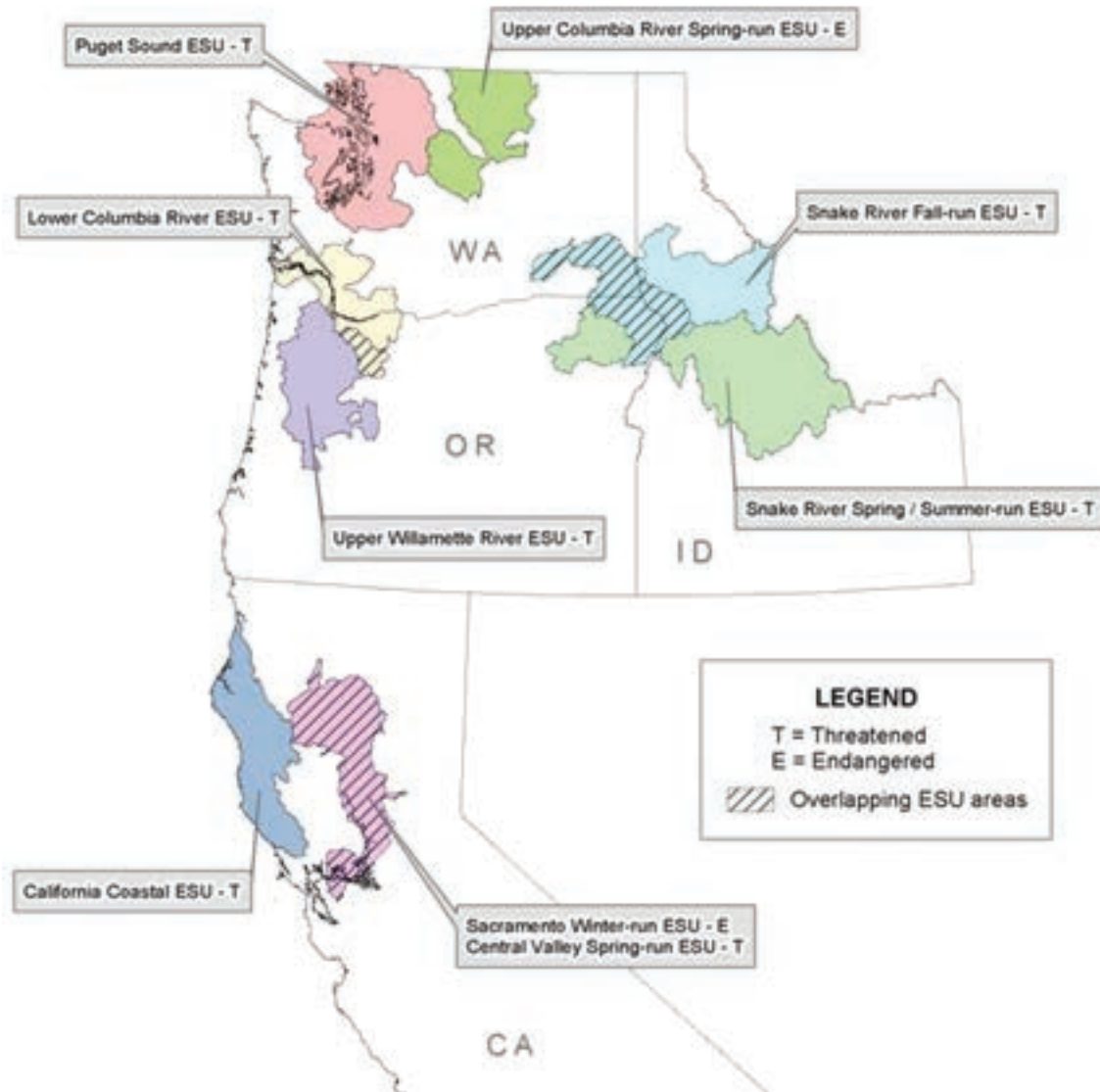

Fig. 2. Geographic drainages of nine Chinook salmon ESUs in the states of Washington, Oregon, Idaho, and California listed either as threatened or endangered under the U. S. Endangered Species Act of 1974. Map by Barbara Seekins, NOAA Fisheries.

Table 3. Threatened and endangered Chinook salmon in the Pacific Northwest listed under the Endangered Species Act (ESA) of the United States.

ESU[1] groups	Year endangered[2]	Year threatened[3]
Sacramento River Winter- Run ESU	1994	1990
California Central Valley Spring- Run ESU		1999
California Coastal ESU		1999
Lower Columbia River ESU		1999
Upper Wilamette River ESU		1999
Upper Columbia River Spring- Run ESU	1999	
Snake River Spring/Summer- Run ESU		1992
Snake River Fall-Run ESU		1992
Puget Sound ESU		1999

[1]ESU or evolutionary significant unit is defined by NMFS as a population that:
    a) is substantially reproductively isolated from conspecific populations, and
    b) represents an important component in the evolutionary legacy of the species.
[2]Endangered means ESU is in danger of extinction.
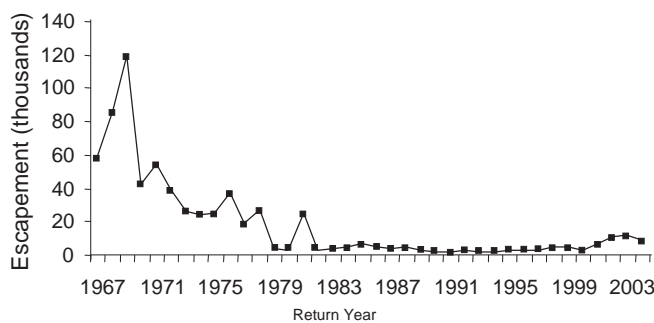[3]Threatened means ESU is likely to become endangered.

Fig. 3. Sacramento River Winter-Run Chinook salmon escapements, 1967–2004. Data from Calif. Dept. Fish Game.
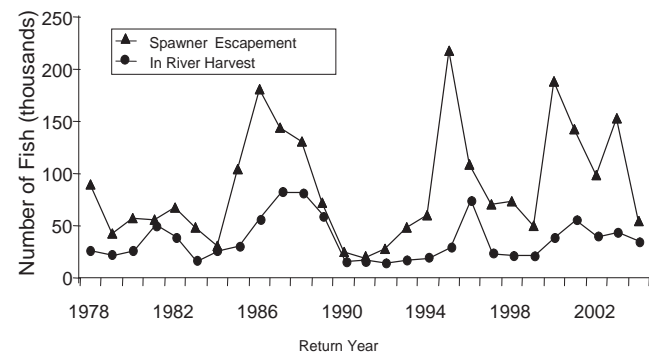

Fig. 4. Escapement and in-river harvest of Klamath River Fall-Run Chinook salmon, 1978–2004. Data from U.S. Fish and Wildlife Service.

Fig. 5. Counts of Spring-, Summer-, and Fall-Run Columbia River Chinook salmon adults past Bonneville Dam, 1977–2005. Data from Columbia River Data Access in Real Time (DART) system (http://www.cbr.washington.edu/dart/adult.html).

River system was not listed under ESA by the BRT, however; this ESU is of concern because of its fluctuations and frequently low escapements. Current runs of Chinook salmon into the Klamath River drainage system are characterized by significant recreational and subsistence fisheries on the river (Fig. 4).

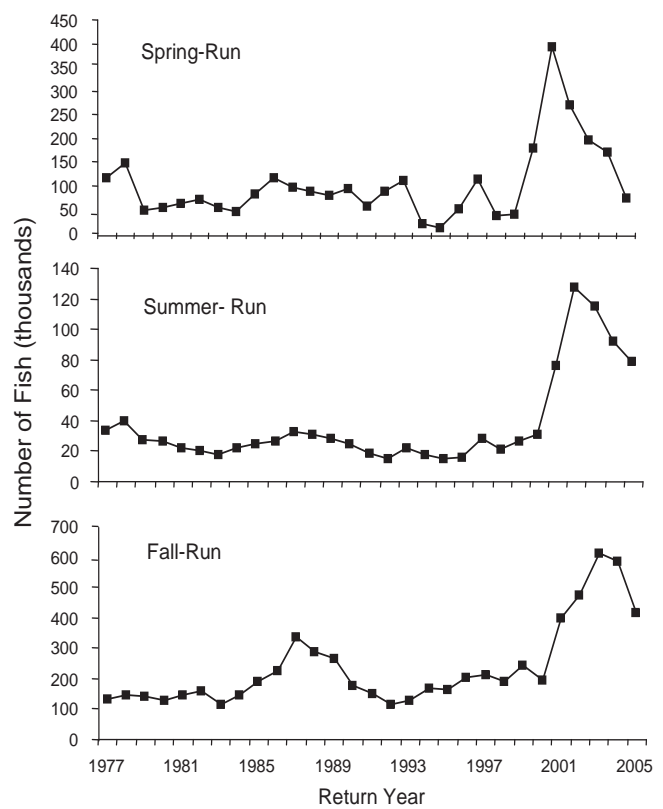There are over 40 dams in the Columbia River Basin, and the first dam encountered by salmon returning from their ocean migration is Bonneville at river kilometer (Rkm) 235. Daily counts of upstream-migrating salmon and other anadromous fishes passing through this dam provide the
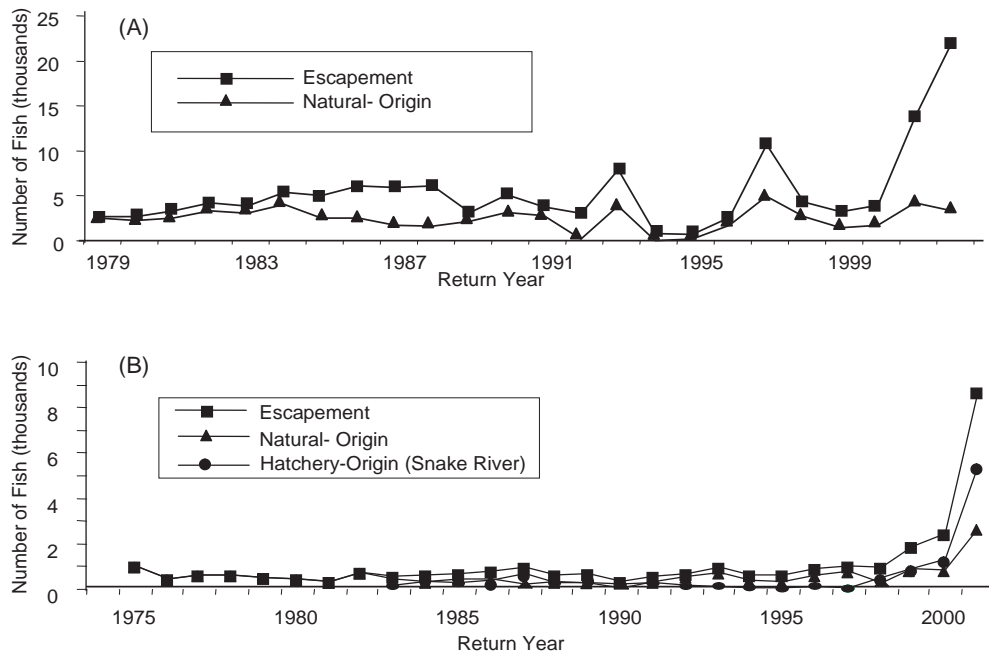
Fig. 6. Escapements of Snake River Chinook salmon past Lower Granite Dam: (A) total escapement and natural origin escapement of Summer-Run, 1979–2002; (B) total escapement, natural origin escapement, and Snake River hatchery origin Fall-Run, 1975–2001. Data from Anonymous (2003a, Figs. A.2.1.1 and A.2.2.2).
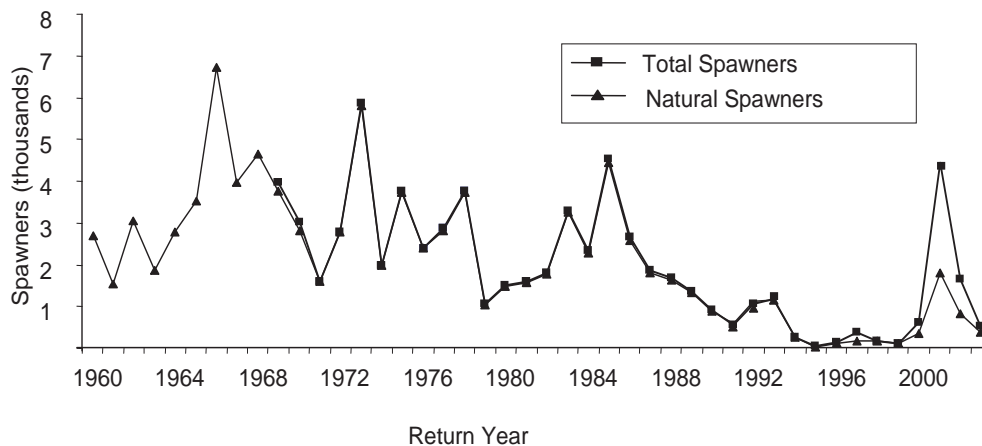

Fig. 7. Estimated number of Chinook salmon spawners in the Wenatchee River, a key indicator stock for the Upper Columbia River Spring-Run ESU, 1960–2003. Data from Anonymous (2003a, Fig. A.2.3.1).

number of each species returning to the river each year. Chinook salmon counts at Bonneville Dam are maintained under the DART system (http://www.cbr.washington.edu/dart/adult.html) in a temporal mode representing run-timing of spring-, summer-, and fall-run fish. Bonneville Dam counts of Chinook salmon are usually designated "spring run fish" from March through May, "summer run fish" from June through July, and "fall run fish" from August through November. Chinook salmon counts at Bonneville Dam from 1977–2005 show a significant increase in returns beginning in 2000 and 2001. However, more recently counts have begun to decline, especially for spring- and summer-run fish (Fig. 5).

The Lower Granite Dam, located on a major tributary of the Columbia River at Snake River Rkm 173, is the last major dam salmon pass before reaching the remaining available spawning grounds in the Snake River Basin. Counts of Chinook salmon at this dam provide assessments on the status of two ESA-listed groups: Snake River spring/summer-run and Snake River fall-run ESUs. Counts of Chinook salmon passing the Lower Granite Dam are evaluated by BRT groups to determine what portion of total escapement is comprised of hatchery salmon and and what portion of natural-origin salmon (Anon. 2003a). The principle of "natural origin" includes both wild salmon and naturally spawning salmon

that may have some measure of hatchery parentage. The distinction between hatchery- and natural-origin salmon is drawn because ESA seeks to foster rebuilding programs with naturally spawning fish and, where possible, to minimize the influence of hatcheries. Snake River summer-run Chinook salmon escapements past the Lower Granite Dam illustrate the differences between total escapement and natural-origin fish (Fig. 6A). When monitoring the Snake Rive fall-run escapement, one of the more contentious Columbia Basin listings, BRT assessors track an additional level of escapement by distinguishing hatchery-origin fish from Snake River stocks (Fig. 6B). Unfortunately, current BRT assessments past the Lower Granite Dam do not include Snake River stock calculations for the most recent years (2003–2005).

Wenatchee River Chinook salmon represent one of the last vestiges of the large Upper Columbia River spring run ESU that was all but totally extirpated with the completion of the Grand Coulee Dam in 1941. BRT estimates of Chinook salmon spawning in the Wenatchee River show a long, steady decline that, even with hatchery supplementation, now includes only a few hundred natural-origin fish (Fig. 7).

British Columbia–Yukon

In a review of Chinook salmon in British Columbia and the Yukon Territory, Slaney et al. (1996) identified from a total of 866 stocks 17 stocks as extinct and 60 others at high or moderate risk of extinction. Slaney's stocks at risk included, among others, some populations near West Vancouver Island, the Strait of Georgia, and certain Fraser River stocks. Concern over declines in population remains today. Canada currently has a two-step system for listing stocks at risk of extinction. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is a committee comprised of representatives from government, academia and other non-governmental organizations, which assesses the risk of a species' extinction. It can then recommend that the federal government place the endangered species under the legal protection of the Species at Risk Act (SARA). If the recommendation is accepted, COSEWIC formulates a recovery plan. COSEWIC's determinations of stock status are somewhat different from those definitions used by Slaney et al. (1996). Presently, there are no Chinook salmon stocks listed under SARA in Canada. Henderson and Graham (1998) attributed overall increases in spawning escapements of Chinook salmon in British Columbia in the late 1980s and 1990s to implementation of the Pacific Salmon Treaty as well as other actions taken in Canada to address domestic conservation concerns. This general increase in abundance has continued since the new regulations were implemented.

Fortunately, the Fraser River, unlike the Columbia River, has no main-stem dams to impede migration of salmon stocks throughout the basin. Like Columbia River salmon, Fraser River Chinook salmon cycle through as spring-, sum-

Fig. 8. Escapements of Fraser River Chinook salmon, Spring- and Summer-Run by life-history type,1975–2004, and Fall-Run, 1984–2004 (Anonymous 2005b).

Fig. 9. Escapements of Fall-Run Chinook salmon in the Strait of Georgia: (A) an index of escapements for a group of stocks in the upper strait, 1977–2004; (B) escapement in the Cowichan River in the lower strait, 1981–2004 (Anonymous 2005b).

mer- and fall-run types. As in the Columbia River, each of these runs is comprised of many individual stocks that exist at different levels of stability or decline. Ocean age .2 and age .3 spring-run Chinook salmon escapements of stream-type spawners in the Fraser River show similar escapement trends but exhibit different levels of abundance, whereas ocean age .3 summer-run fish from both stream and ocean-type spawners show similar escapement trends and similar abundance levels (Fig. 8). Both spring-run and summer-run Chinook salmon show a decline in escapements from recent highs in the Fraser River. Fall-runs have demonstrated considerable year-to-year fluctuation (between 100 and 200 thousand fish)

Fig. 10. Chinook salmon EV and CWT cohort survival indices for Strait of Georgia hatcheries, 1974–2003, including Quinsam Hatchery in the upper strait and Big Qualicum, Puntledge, and Cowichan Hatcheries in the lower strait. EV indices are scalers generated by the PSC coastwide Chinook salmon model which reflect annual variability in natural mortality in the initial year of ocean residence while CWT indices represent survival of CWT-marked releases to age two. Standardized EV scalers are plotted for complete and incomplete broods,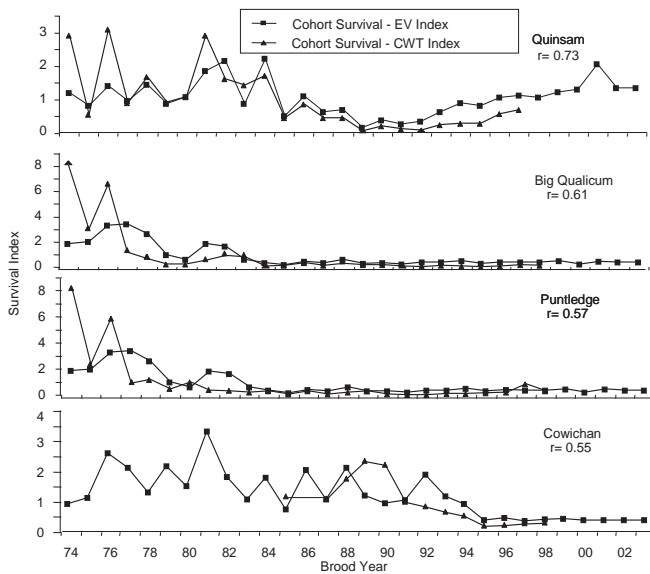 while only completed brood values are plotted for CWT survivals; the r value is the correlation coefficient between the two indices, which indicates that the two generally track one another. Data from CTC files.

with no clear long-term trend (Fig. 8). The Harrison River stock, which comprises the vast majority of this stock group, represents one of the largest single Chinook salmon stocks in the Pacific Northwest.

Perhaps the most recent conservation concern in Canada is Chinook salmon in the Strait of Georgia. While CTC assessments indicate low abundance levels throughout the Strait of Georgia, there are discernable regional differences between the Upper Georgia Strait (UGS; relatively higher) and the Lower Georgia Strait (LGS; relatively lower), in population trends, and in survival rates (Anon. 2003b, 2004b). Generally difficult to enumerate, the UGS group consists largely of stocks heavily influenced by glacial run-off. While there is evidence that the UGS group has increased in abundance since the late 1990s, this observation may be confounded by a concurrent change in enumeration methodology for this stock group (Fig. 9A). The LGS stock group, however, has undergone continuous declines over the past decade. The stock group's status is primarily monitored via returns to the Cowichan River, which has traditionally been the largest single stock within the stock group. The Cowichan River is monitored for total escapement and natural spawners, because hatchery-origin fish may also spawn in the river. Escapements to the Cowichan have declined precipitously since the mid-1990s (Fig. 9B).
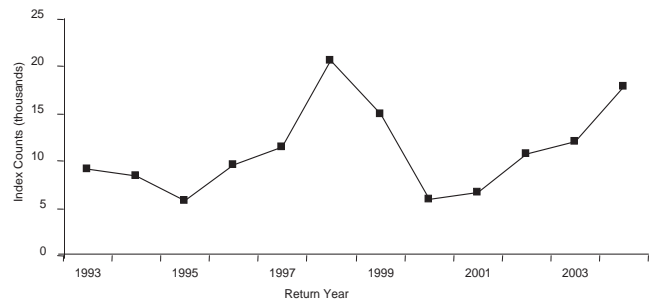

Fig. 11. Escapement index counts of Chinook salmon for 14 West Vancouver Island streams, 1993–2004 (Anonymous 2005b).

A difference in the status of Chinook salmon in UGS and LGS is also apparent in the survival trends of hatchery smolts released in the two regions. The survival rate for smolts released at Quinsam Hatchery in UGS is measured by coded wire tag (CWT) recoveries and an environmental variable (EV) scaler index generated by the PSC coast-wide model (Anon. 2004c); these measurements indicate an improving survival trend since the early 1990s (Fig. 10). In contrast, survival rates among three LGS hatchery stocks (Big Qualicum, Puntledge, and Cowichan) show considerable decline for both CWT and EV indices—in some cases, since the early 1980s—and have remained at these low levels ever since (Fig. 10). These comparisons illustrate a puzzling difference in the status of Chinook salmon in the two regions of the Strait of Georgia. Possible factors that could be contributing to the present condition include: overfishing by commercial and recreational fisheries, changes in the environment (Beamish et al. 2004), shifts in abundance, changes in predators' and competitors' behavior (Beamish and Neville 2000; Beamish et al. 2003), and differences in migration patterns.

One possible difference in survival patterns in the UGS and LGS areas could be the amount of time juvenile and immature Chinook salmon spend in the Strait of Georgia. According to Healey (1980) numerous juvenile, ocean-type Chinook salmon remain in the LGS throughout much of their first ocean year, and, judging from sport fishery catches, juveniles remain plentiful in the LGS during their second ocean year (Argue et al. 1983). However, CWT recovery information indicates that the majority of these fish are from the LGS. Furthermore, based on CWT recoveries of Quinsam-hatchery Chinook salmon, UGS stocks, unlike LGS stocks, are far-north-migrating and are generally intercepted outside the Georgia Strait, suggesting that some deleterious factors within the Strait of Georgia have led to population declines in the lower Strait of Georgia.

Beamish and Neville (2000) identified spiny dogfish and river lampreys as major predators of juvenile Chinook salmon in the Strait of Georgia. They estimated that 1.4 million spiny dogfish ate the equivalent of all 7.7 million juvenile Chinook and coho salmon released from local hatcheries
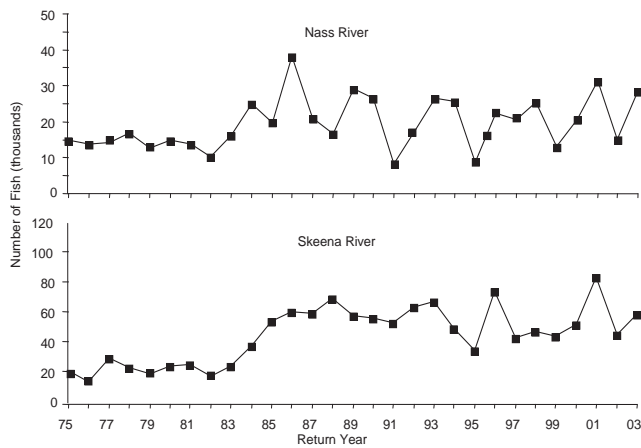
Fig. 12. Chinook salmon escapements for the Skeena and Nass rivers in northern British Columbia, 1975–2003 (Anonymous 2005b).

Fig. 13. Chinook salmon escapements for the Taku and Stikine rivers in southeastern Alaska, 1975–2003 (Anonymous 2005b).

Fig. 14. Chinook salmon escapements for the Kenai River in south-central Alaska, 1986–2004. Data from ADF&G Sport Fish Division.

in 1988, and that 3.0 to 3.9 million river lampreys killed 20 million and 18 million juvenile Chinook salmon in 1990 and 1991, respectively (Beamish and Neville 2000). Ford and Ellis (2005) found that fish-eating killer whales residing in the Strait of Georgia have a strong preference for Chinook salmon throughout much of the year, especially in the LGS. Ford and Ellis (2005) suggested that this preference for Chinook salmon could influence the year-round distribution patterns of resident killer whales within the Strait of Georgia. Selective predation is only one factor that may cause differences in the survival rates of LGS and UGS Chinook salmon stocks.

Another Chinook salmon stock group of conservation concern in British Columbia is found on the west coast of Vancouver Island. This group consists of several dozen small, coastal fall-run populations. A 14-stream index is used to monitor the abundance of this stock group (Anon. 2003b; 2004b). While this index shows modest increases in the last four years (Fig. 11), these populations are still of concern because several individual stocks in the group remain at very low levels.

In general, the abundance of Chinook salmon stocks in central and northern British Columbia has been relatively stable. This stability is illustrated by Nass and Skeena river returns, the two largest stock aggregates in northern British Columbia. While returns to the Nass have remained stable, those to the Skeena have improved since the signing of the PST (Fig. 12).

Alaska

In contrast to declining trends in Chinook salmon's abundance in WOIC and some areas in British Columbia, most salmon populations throughout Alaska are stable. Baker et al. (1996) identified 63 spawning aggregates of Chinook salmon in southeastern Alaska and, of the 31 groups with sufficient data for evaluation, they found only one that exhibited a de-

clining escapement trend. Burger and Wertheimer (1995) and Wertheimer (1997) found that commercial harvests of Alaskan Chinook salmon have remained relatively stable over time when compared to harvests of other species. In southeastern Alaska, the Chinook salmon fishery is dominated by commercial trolling, and a large portion of the harvest in the region originates from more southerly, non-Alaska stocks. Harvesting of the region's Chinook salmon is regulated by catch limits and treaty oversight. Although Chinook salmon are the first to return to Alaska's rivers each year, commercial fisheries are normally allowed to target only those fish in terminal areas of a few river systems (Heard and Anderson 1999). After a lengthy period of fishery closures and stock rebuilding under PSC oversight, limited commercial gill-net fisheries were allowed in 2005 to target Chinook salmon returning to the Stikine and Taku rivers.

Escapement trends for stock groups in two of southeastern Alaska's largest drainages (Taku and Stikine rivers) show relatively stable patterns (Fig. 13). These trans-boundary rivers originate either in British Columbia or the Yukon Territory and fall under PSC oversight. In the Cook Inlet region of south-central Alaska, Kenai River Chinook salmon that support a major in-river sport fishery participate in early and late runs, spawning in upper and lower portions of the

Fig. 15. Chinook harvest from Bristol Bay and from the Kuskokwim and Yukon rivers in western Alaska, 1980–2004. Data from ADF&G Commercial Fish Division.

Fig. 16. Chinook salmon harvest from the Kamchatka Peninsula in Russia, 1934–2005: (A) total harvest; (B) harvest from east and west Kamchatka. Data from SakhNIRO.

drainage. Escapements to both run segments show relatively stable trends (Fig. 14).

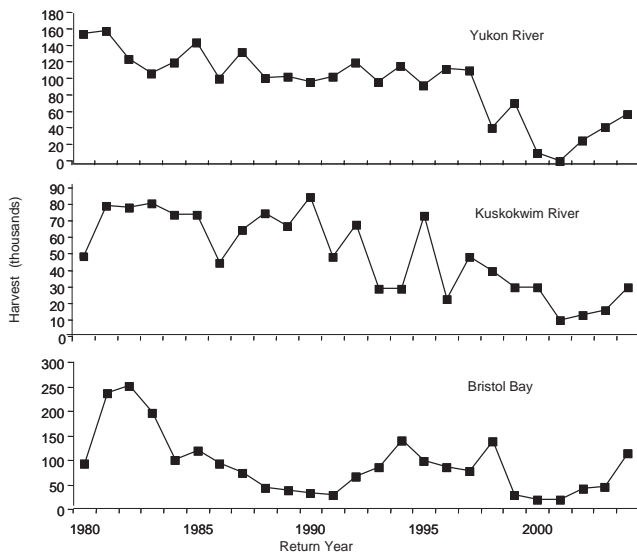Western Alaska represents the region in Alaska where there is most concern over trends in abundance of Chinook salmon. Long-term data sets on escapements in this region are somewhat spotty, therefore, harvest data are used to assess trends, although these data may not reflect true abundance trends. Harvest data from Bristol Bay, and the Kuskokwim and Yukon rivers all suggest declining abundance (Fig. 15). Although overall harvests in Bristol Bay show a downward trend, the commercial fishery mainly targets Nushugak River stocks that are still thought to be relatively healthy. Declining catches in both the Kuskokwim and Yukon rivers is a matter for concern for rural Alaskans living in these regions. Chinook salmon runs into the Yukon River, another transboundary river originating in Canada and managed under a separate treaty annex, were so low in 2001 that no commercial fishery was allowed. One area of concern regarding the present status of stocks in the Kuskokwim and Yukon rivers is the Chinook salmon by-catch made from these systems by groundfish trawl fisheries in the Bering Sea.

Russia

On the Asian side of the Pacific Rim, harvest data are also used to look at trends in abundance because precise escapement data is limited. Radchenko (1998) reviewed abundance trends in Russian Chinook salmon and reported that commercial catches had declined from a peak of 3,000 mt in the 1970s to 600 mt in the late 1990s. Commercial catches declined further to 200 mt by 2003 but have begun rebounding in the last two years to their current levels above 500 mt (Fig. 16). Although Chinook salmon fisheries are found on

both the east and west coast of the Kamchatka Peninsula, 80–90% of Russia's total catch comes from eastern Kamchatka, and primarily from the Kamchatka River, whereas catches from western Kamchatka are mostly from the Bolshaya River. Radchenko (1998) suggested that there were several small, unexploited stocks in western Kamchatka that could increase the commercial catch up to 100 mt if exploited. In recent years, the total run—catch plus escapement—of Chinook salmon off both the east and west coasts of the Kamchatka Peninsula has been estimated by Shevlyakov to be at 170–190 thousand fish annually. Only in a few smaller rivers (Koly, Pymta, and Kikhchik) have adult escapements been at favorable levels in recent years. The major river systems (Kamchatka and Bolshaya) appear to have had inadequate escapements over the past decade due to intense fishing and increased in-river poaching.

The run timing of Chinook salmon returning to spawn in Russian rivers follows a late spring/summer-run pattern. In the Kamchatka River the commercial fishery begins operating shortly after the ice breaks up in May, and its operation peaks in June (Vronskiy 1972). Chinook salmon in the Kamchatka River also migrate in early and late runs. Some early-run fish may enter the river in spring before the ice is out. The run timing of the early run extends from late May to mid-June with spawning occurring from mid-June through August and peaking in late July to early August. Run timing of the late run extends from early July to late August with spawning occurring from mid-August to mid-September and peak spawning occurring in late August. Stream-type Chinook salmon are typical of populations in Asia although some under-yearling juveniles do migrate to sea from Kamchatka Peninsula rivers. However, adult returns for such stocks are extremely poor.

BIOLOGICAL CHARACTERISTICS

Chinook salmon are an extremely plastic species with the most diversified and complex life history among Pacific salmon. The species has many unique biological characteristics including highly evolved and diversified run timing (Waples et al. 2004) with adults entering rivers and spawning in almost every month of the year, exhibiting stream-type and ocean-type life-history forms with different freshwater and oceanic migration behavior patterns (Healey 1983), and some having both red- and white-fleshed forms (Godfrey 1975; Hard et al. 1989).

The coastal region of northern British Columbia and southeastern Alaska (54°–56°N) represents a transition area where populations with ocean-type life histories generally predominate to the south whereas stream-type life histories predominate to the north (Healey 1983). Upriver populations from longer trans-boundary rivers that penetrate the coastal mountain range in southeastern Alaska exhibit stream-type life histories in fresh water. These populations also display more extensive oceanic migration patterns characteristic of stream-type biology. Other populations of Chinook salmon from shorter rivers restricted to the coastal regions of southeastern Alaska also exhibit stream-type life history in fresh water (i.e. yearling smolts). In contrast, however, while at sea these coastal populations tend to exhibit an ocean-type life-history behavior by foregoing distant open oceanic migrations and instead remaining in coastal waters. Such transitional behavior in fresh water and marine life histories could result from a predisposition for ocean-type life history based on genetic origin modified by environmental constraints requiring extended freshwater rearing at higher latitudes. Guthrie and Wilmot (2004) speculated that cooler northern climates could cause this type of a life-history shift. Gharrett et al. (1987) suggested that, based on the intermediate genetic composition of Chinook salmon populations, the salmon in the region could have come from two different refuges in their post-glacial colonization. Based on current life-history behavior patterns, it seems likely that under such a scenario, coastal populations seaward of the coastal mountain range in southeastern Alaska arose from ancestral ocean-type parents, while longer-migrating, upriver populations (i.e. in the Taku, Stikine, and Alsek rivers) arose from stream-type parentage.

An important life-history characteristic in Chinook salmon is long-term change in size and age. Ricker (1980) pointed out that Chinook salmon had decreased in average size by 50% or more during the twentieth century. Potential contributing causes include the selective effects of fisheries, changes in oceanic environments, habitat loss, dams such as the Grand Coulee that eliminated entire runs of large fish, and the prevalence of contemporary hatchery production in many areas. According to Ricker (1980, 1981), fisheries—especially troll fisheries—which capture both immature and maturing fish, ultimately bring about a decrease in propor-

tions of older, larger fish in spawning populations and an increase in younger, smaller fish. Ricker believes that declines resulted from a progressive deterioration of the genetic basis for maturation at older ages. A somewhat-related process may also be underway when hatchery-produced fish return at a reduced size per age and earlier in run-timing in comparison with naturally spawned fish. Increased maturation timing in hatchery fish is partly due to accelerated growth of juveniles in the hatchery environment (Larson et al. 2004). In some supplementation programs, however, hatchery males and females are returning not only earlier but also at smaller sizes than naturally-spawned fish in both Chinook salmon (Anon. 2004a; Pearsons et al. 2004), and in steelhead (Mackey et al. 2001).

In a later study Ricker (1995) noted that, by the early 1990s, declines in size of Chinook salmon catches (particularly 1951 through 1975) had been fully reversed or at least arrested in many but not all areas. Dramatic reversals were

Fig. 17. Average weights of Chinook salmon caught in regional Alaska fisheries, 1994-2004. AAH is average annual harvest in thousands of fish for each region. R^2 values measure how well the regression line fits data in the trend line. Data from ADF&G Commercial Fish Division.

Fig. 18. Average weights of the 30 largest Chinook salmon caught in a May sport fishing derby near Juneau, Alaska, 1998–2005. R^2 measures how well the regression line fits data in the trend line. Data from Tlingit-Haida Central Council.

Fig. 19. Composition of Kamchatka River Chinook salmon by life-history types, 1958–2004. Data from KamchatNIRO.

Fig. 20. Average weight of Kamchatka River Chinook salmon spawners by decade, 1958–2004. Data from KamchatNIRO.

evident in Canadian troll catches in Areas 1 and 5, but less so in Area 12. Dominated by troll fisheries, all Chinook salmon gear catches in southeastern Alaska showed similar improvements in size, whereas all gear catches in Puget Sound showed only minor improvement. Ricker expressed puzzlement over possible causes of these size reversals in certain areas. He indicated that changes in fishing regulations and minimum size limits are of special importance for troll fisheries since many Chinook salmon are caught while still growing rapidly, and he suggested that the factor or factors responsible for the size reversal might be apparent if age composition data were available (Ricker 1995).

Bigler et al. (1996) found that seven of nine individual or aggregate populations of Chinook salmon between 1975 and 1993 had decreased in average size. The increase in average size observed by two commercial troll fisheries in California and British Columbia may have been the result of changes in fishery regulations (e.g. size limits were increased in British Columbia's troll fisheries in 1987). The average weights of Chinook salmon in several Alaskan commercial fisheries from 1994 to 2004 continue to show declines (Fig. 17). A recreational fishery for Chinook salmon in the vicin-

ity of Juneau, Alaska, primarily targets returning Taku River spawners during the month of May. The average size of the largest 30 fish caught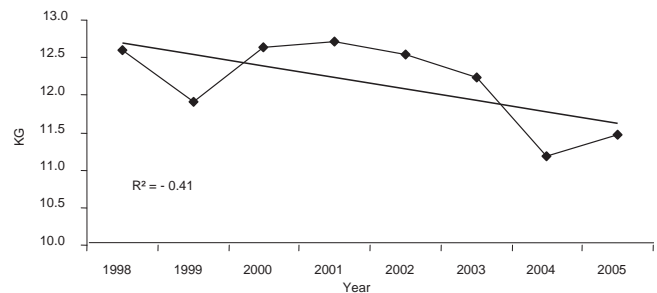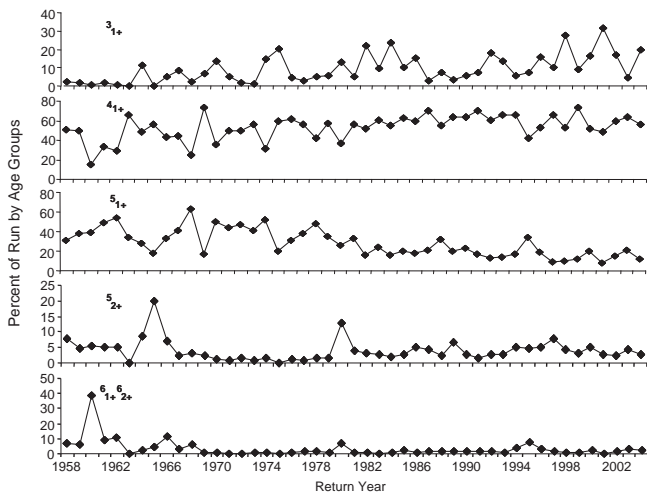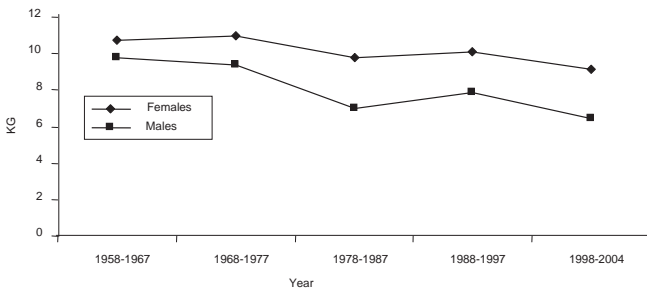 from 1998 to 2005 show a declining trend (Fig. 18). From 1958 to 2004, the percentage of older Chinook salmon in the Kamchatka River has decreased while the percentage of younger fish has increased (Fig. 19). These dramatic changes in age structure are accompanied by modest decreases in the average size of returning fish, a trend that is more pronounced in males than females (Fig. 20).

CONCLUSIONS

The present population of Chinook salmon stocks from around the Pacific Rim varies considerably according to different geographic regions. For example, in the U.S. Pacific Northwest states of Washington, Oregon, Idaho, and California, where nine stock groups are currently listed by the ESA as threatened or endangered species, many wild stocks remain at or near record low levels. Other stocks in this area are already extinct due to a long list of contributing factors, including over-fishing; loss of spawning and rearing habitats; impediments to upstream or downstream migration due to river dams; watershed logging; water allocations for farming, mining and navigation; and generalized industrialization and urbanization throughout the region. Over time, recovery programs for some ESA-listed stock groups in the Sacramento and Columbia rivers are beginning to cause minor improvements.

While no Chinook salmon stocks are legally protected under the Canadian COSEWIC and SARA programs, some stocks in southern British Columbia, especially in the Lower Strait of Georgia and West Vancouver Island, are of special concern. The status of stocks in central and northern British Columbia are either stable or improving, due, in part, to conservation measures implemented since the PST was signed in 1985.

Chinook salmon stocks throughout most of Alaska are comparatively stable with the exception of stocks in the Kuskowim and Yukon rivers in the western part of the state. The by-catch of these stocks in Bering Sea groundfish trawl fisheries is an issue of concern. Stocks in the southeastern portion of Alaska have also benefited from PST conservation and managerial oversight.

As reflected by harvest trends, Russian stocks of Chinook salmon on the Kamchatka Peninsula have declined from 3000 mt in the 1970s to around 500 mt currently. Russia's two major river systems (Kamchatka and Bolshaya) appear to have had serious declines in escapement size over the past two decades due to intense fishing and in-river poaching.

Historically, hatcheries have played significant, and often controversial, roles in many Chinook salmon issues—especially in the U.S. Pacific Northwest and southern British Columbia. The use of hatcheries to mitigate anthropogenic-caused declines in wild stocks is now viewed as counterproductive to the long-term health and genetic diversity of

salmon species. Nevertheless, many hatcheries today are implementing important changes in past practices and operate under more clearly defined objectives to help rebuild depressed wild runs or to help support certain fisheries. Hatcheries continue to play a major role in many important Chinook salmon populations and fisheries.

The selective harvesting of both immature and older, larger Chinook salmon in various fisheries, habitat loss, the extirpation of certain stocks of large fish, variable growth conditions in marine environments, some hatchery practices, and long-term environmental changes may all be interacting to cause significant long-term reductions in the average size and age of Chinook salmon .

Given the complex life history and plasticity exhibited by Chinook salmon, it is not surprising that this species may be responding to warming climatic conditions in Arctic environments by expanding its range into new regions, especially into the Beaufort Sea drainages of North America. Previous accounts of collections have been reported for the Mackenzie River (Mcleod and O'Neil 1983) and the Coppermine River (Hart 1973) in the Canadian Arctic. Other recent developments suggest that the species is also becoming more prevalent in Arctic regions of Alaska. These developments include recent catches of 20–25 adult Chinook salmon annually by subsistence fisheries in Elson Lagoon near Point Barrow (C. George, Dept. of Wildlife Mgmt., North Slope Borough, P.O. Box 69 Barrow, AK 99723, pers. comm.) and the collection of four adult Chinook in Ublutuoch River, a tributary stream near the mouth of the Coville River, AK, in 2004 (Moulton 2005).

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Trends in Abundance and Size of Coho Salmon in the Pacific Rim

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Abstract: In the early 1960s, average Pacific-wide landings of coho salmon reached a stable level of over 12 million fish that persisted for 3 decades, followed by a sharp decrease to under 6 million fish in 1997–2003 as a result of reduced marine survival and fishery restrictions in the Pacific Northwest and British Columbia. Spawning escapement increased in most streams after 1999 in response to restricted fishing and improved marine survival for some stocks. Marine survival has been spatially and temporally variable, accounting for an average of 54% (range 41–68%) of variation in wild adult returns to twelve systems from Washington to southeast Alaska. Average survival rates have been highest (> 12%) in southeast Alaska and Puget Sound, and lowest (4–6%) for the Washington coast, with British Columbia being intermediate (6–10%). Marine survival was highly variable over a limited spatial scale, indicating that localized marine environments are critically important to overall ocean survival. The average weight of coho salmon harvested in Alaskan fisheries has changed little since the 1960s, but indicators of average weight in southern British Columbia to the Columbia River declined from the 1950s to early 1990s, followed by a rapid rebound from 1993 through 2004.

Keywords: coho salmon, abundance, survival, escapement, size

INTRODUCTION

Spawning populations of coho salmon are currently distributed around the Pacific Rim from Monterey Bay in central California to the Russian Far East (Sandercock 1991). The species' protracted stream residence makes it sensitive to changes in its freshwater habitat. Human development has reduced the productive capacity of many watersheds from California to southern British Columbia (Beechie et al. 1994; Brown et al. 1994; Weitkamp et al. 1995; Bradford and Irvine 2000). However, widespread development of hatchery production during the 1970s and 1980s acted to offset reductions in natural stocks (Mahnken et al. 1998).

Compounding the effect of long-term changes in habitat productivity have been large variations in survival of smolts entering the ocean (Coronado and Hilborn 1998; Beamish et al. 2000). During the 1990s, very poor ocean survival helped drive natural stocks to low levels that threatened the continued existence of some populations, and stocks in several areas of the Pacific Northwest and Canada were listed as threatened or endangered (Good et al. 2005). Fisheries were curtailed in response to these declines and listings (Chen and

Holtby 2002), and harvest-based measures of the species' status are no longer informative for southeastern portions of its range. At the same time, assessments based on catch for regions west of southeast Alaska have indicated a trend of strong returns to Alaska since the early 1980s and a decline in the Russian Far East since the early 1990s (Radchenko 1998; Geiger et al. 2002; Eggers et al. 2005).

Detailed stock information has played an increasing role in stock assessments from southeast Alaska to California (Brown et al. 1994; Weitkamp et al. 1995; Henderson and Graham 1998; Kope and Wainwright 1998; Anonymous 2002a; Shaul et al. 2004). Several intensively monitored populations, or indicator systems, in southeast Alaska, British Columbia and Washington provide detailed information on escapement, smolt production, marine survival, return abundance, exploitation rates and return/spawner. Populations that have been monitored for a decade or more are useful indicators for both fishery management and environmental change. In areas such as the Oregon coast, where fishing on wild stocks has been curtailed and where no indicator stocks exist, assessment of the recent abundance of natural stocks depends primarily on estimates of spawning escape-

ment (Anonymous 2005). However, escapement information is very limited to non-existent in Alaska and the Russian Far East because of the logistical difficulty of measuring the number of spawners during wet fall months in widely scattered, remote systems. Given these considerations, an assessment of coho salmon abundance across the North Pacific Rim depends upon different types of information for different regions.

COMMERCIAL CATCH TRENDS

The total Pacific commercial catch increased gradually from the mid-1920s and reached a plateau in the early 1960s, averaging 12.5 million fish from 1962 to 1994 based on data reported by Eggers et al. (2005) and shown in Fig. 1. From the mid-1950s to late 1970s, the Japanese high seas catch averaged over 3 million fish annually, representing a quarter of the total Pacific catch. The inshore harvest increased near the end of the high seas fishery, averaging 11.4 million fish from 1979 to 1994 and peaking at 16.0 million fish in 1986 before declining precipitously to a record low harvest of only 4.5 million fish in 1997. Following 1997, the total harvest increased gradually to 7.1 million fish in 2004. The decline in harvest in the mid-1990s was attributed primarily to se-

vere fishing restrictions in Washington, Oregon and California beginning in 1992 and in British Columbia beginning in 1996–1998. Meanwhile the average harvest in southeast Alaska increased slightly from 2.6 million fish in 1980–1996 to 2.8 million fish in 1997–2004 (Fig. 1). Alaska accounted for an average of 77% of the total Pacific coho salmon harvest during 1997–2004, compared with only 15% during a period of low Alaskan production in 1955–1977.

Commercial harvests in the Pacific Northwest (California, Washington, and Oregon) were at first steady and then increased slowly from 1925 until the 1970s, reaching peaks of over 4 million fish per year in 1971, 1974 and 1976 (Fig. 2). The harvests in that region remained strong until the early 1990s, but plummeted after 1991 due to poor returns and restricted fisheries (Weitkamp et al. 1995). Commercial harvests in southern British Columbia followed a similar trend but were not curtailed until the mid-1990s in response to the deteriorating status of local stocks including those of the Thompson River, a Fraser River tributary (Bradford and Irvine 2000). The steadily increasing harvests in southern British Columbia through the 1980s resulted from a combination of stable fishing opportunities and increasing hatchery releases that peaked in the mid-1980s (Mahnken et al. 1998).
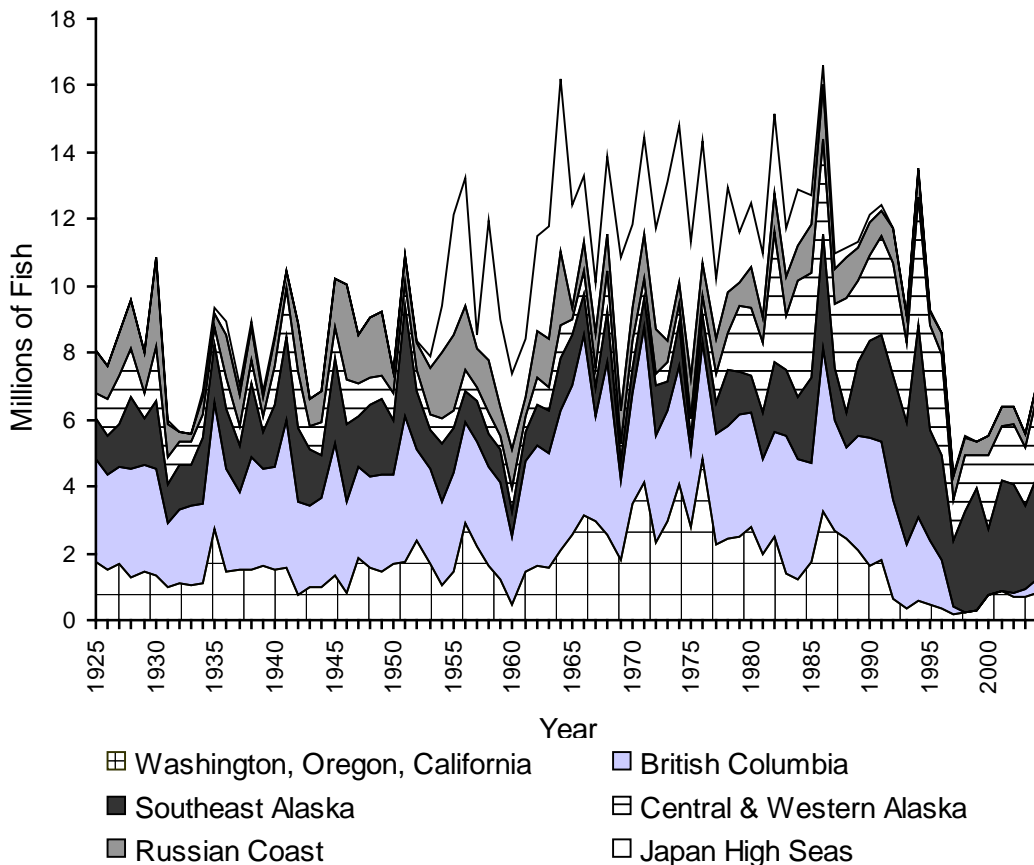

Fig. 1. Total commercial landings of coho salmon in the Pacific Rim, 1925–2004.
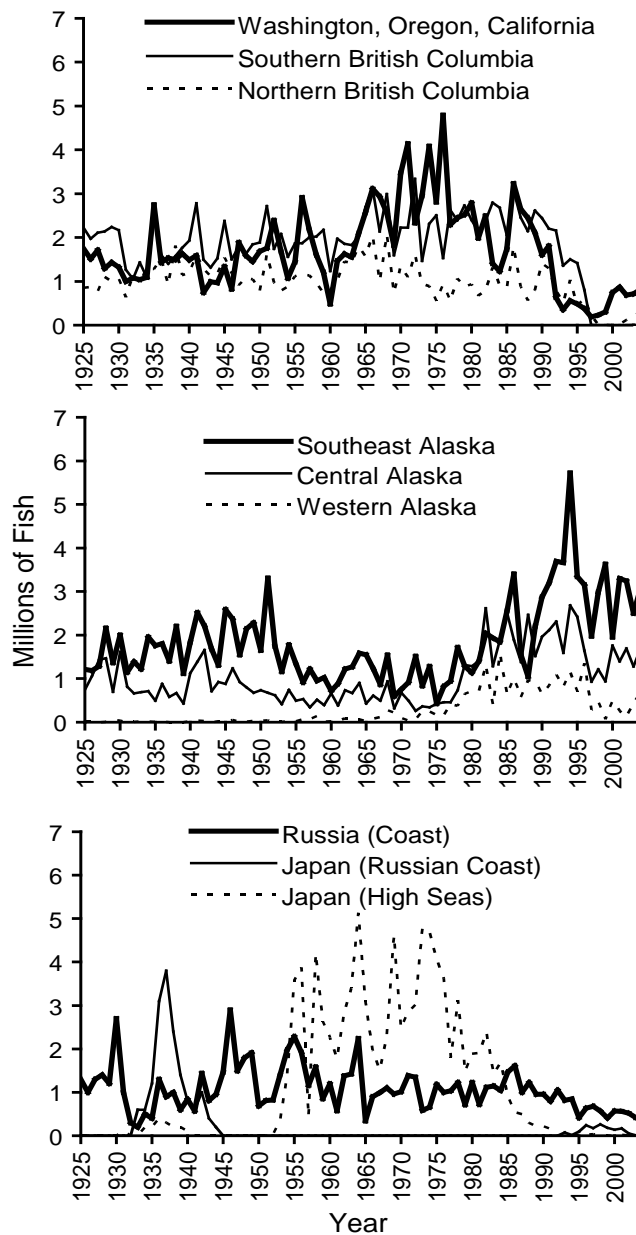
Fig. 2. Commercial harvest of coho salmon by region, 1925–2004.

Fig. 3. Commercial catch of wild coho salmon in southeast Alaska and all coho salmon (including a very small hatchery component) in northern British Columbia, 1900–2004.

The harvest in northern British Columbia, comprised mostly of local wild stocks, followed a stable trend from the mid-1920s until the mid-1990s. Fisheries in that region were severely restricted after the extremely poor 1997 run that produced the lowest harvest since 1905. In contrast, the southeast Alaska catch declined sharply in the early 1950s and remained depressed through the late 1970s, but rebounded beginning in 1982. A significant factor in the recent increase has been hatchery production that developed rapidly in the 1980s and stabilized after 1990 at about 20% of the total commercial harvest (Shaul et al. 2004). Relatively stable fisheries on wild, locally produced stocks in northern British Columbia and southeast Alaska display a synchronous tem-

poral pattern interrupted by major shifts in scale spanning a five-fold range of catch multipliers between the regions (Fig. 3). These shifts in 1954–1955, 1976–1977 and 1991–1992 are delineated by best-fit linear regressions as found in Fig. 4.

The second major shift occurred closely coincident with the well-documented 1977 regime shift (Beamish and Bouillon 1993; Francis and Hare 1994; Hare and Mantua 2000). However, there was an equally pronounced shift in the early 1990s preceding a period of very poor harvests in northern British Columbia compared with southeast Alaska in 1992–1997. Harvests in central Alaska fisheries from Prince William Sound to the Alaska Peninsula showed a similar increase to harvests in southeast Alaska after 1977, but have declined since 1997, while southeast Alaska harvests have remained high (Fig. 2). Development of commercial fisheries for coho salmon on many western Alaska systems draining into the Bering Sea did not occur until the late 1960s and 1970s. Harvests in the area were typically high during 1982–1996, but declined sharply in the late 1990s with poor returns to some systems. Low salmon prices in recent years have also constrained exploitation of many central and western Alaska stocks, particularly in more remote areas.

Russian coastal harvests of mostly wild coho salmon followed a very stable long-term trend from 1925 through 1992, around an average harvest of 1.15 million fish (Fig. 2). After 1992, however, harvests declined and averaged only 0.50 million fish in 2000–2004. Radchenko (1998) attributed the likely cause to an increase in illegal fishing on
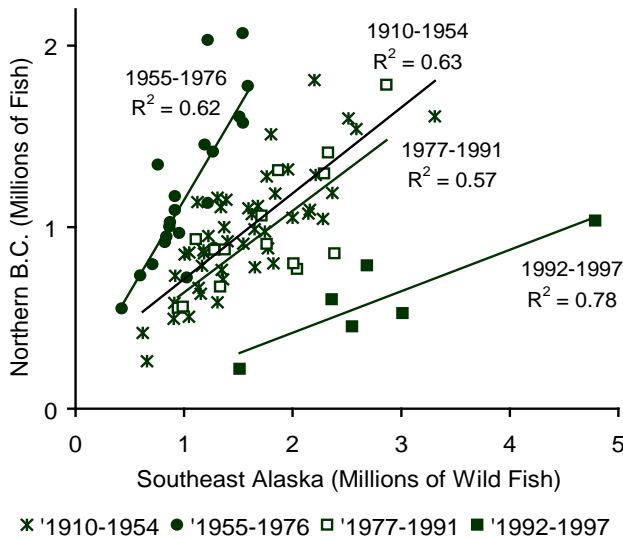
'1910-1954 ● '1955-1976 □ '1977-1991 ■ '1992-1997

Fig. 4. Linear relationship between the commercial catch of wild coho salmon in southeast Alaska and all coho salmon in northern British Columbia apportioned into periods with best statistical fit, 1910–1997.

Fig. 5. Commercial catch of wild coho salmon compared with pink salmon in southeast Alaska, 1955–2005. The time series is divided into four periods that correspond with smolts entering the sea during recognized regime periods (< 1977, 1977–1988, 1989–1997 and 1998–2004).

Fig. 6. Number of coho salmon released from Alaska, British Columbia and Pacific Northwest hatcheries, 1952–2004.

the spawning grounds. Small Japanese harvests along the Russian coast have averaged 0.12 million fish since 1993 but have not substantially offset the decline in the Russian harvest.

An informative comparison can be made between species within southeast Alaska. Coho and pink salmon are naturally abundant in streams throughout the region and both species spend slightly over a year at sea, so their returns reflect a similar experience in the ocean. Despite being exploited primarily in independent fisheries involving different gear, the relationship between the two species in the commercial harvest has been relatively consistent for over 50 years (Fig. 5), with the only substantial outlying observation being the record 1994 wild coho salmon harvest that corresponded with a large, but not exceptional, pink salmon harvest. A substantial upward shift in abundance became evident after 1981 and catches remained very high on average following the 1989 regime shift (Hare and Mantua 2000). However, there is no clear effect of a regime shift in 1998 (Peterson and Schwing 2003). Since 1990, low coho and pink salmon harvests approaching those during 1955–1977 have occurred only twice, in 1997 and 2000.

HATCHERY RELEASES

Hatchery production of coho salmon in western North America began around 1900 (Mahnken et al. 1998) but remained very limited until the 1950s and 1960s when advances in culture techniques led to improved post-release survival of hatchery fish (Lichatowich and McIntyre 1987). Hatchery releases in the Pacific Northwest and British Columbia of all life stages comprised primarily of smolts increased rap-

idly in the 1970s and peaked in the Pacific Northwest at 167 million fish in 1981 (Fig. 6) based on data reported by the Pacific States Marine Fisheries Commission. Alaskan production reached 1 million fish released in 1972 and increased until the late 1980s before stabilizing. The coast-wide peak of nearly 181 million fish was achieved in 1985 when Canadian hatcheries boosted smolt output to improve recreational fishing for the 1986 World Exposition in Vancouver. Coast-wide releases remained relatively stable from 1987 to 1992 at 136–159 million fish, and then declined to 76 million in 2004. Releases from Oregon and Alaskan facilities have remained relatively stable since 1997 at about 8–10 million

fish in Oregon and 18–22 million fish in Alaska. Meanwhile, Washington production declined from 95 million fish in 1992 to 44 million fish in 2002 followed by a marked drop to 37 million fish in 2003 and only 34 million fish in 2004. British Columbia releases remained stable at 18–24 million fish from 1986–2002 but also declined markedly in 2003 and 2004.

TOTAL ABUNDANCE ESTIMATES

Direct estimates of the total number of returning adults are available for only a few systems in most regions. However, working estimates of total abundance of wild and hatchery fish are available for some geographic areas including Puget Sound, the Washington coast and a grouping of hatchery and wild catches and escapements known as the Oregon Production Index (Anonymous 2005). Run size estimates are shown as a proportion of the 1993–2003 average in order to compare temporal patterns among systems with widely varying production capabilities (Fig. 7).

The Oregon Production Index peaked in the early to mid-1970s at an average of nearly 3 million returning adults before declining to a lower but relatively stable average of about 1.6 million fish in 1977–1991. In the early 1990s, the index declined even more dramatically to an average of only 323,000 fish in 1993–1999 before rebounding to an average of about 1.1 million fish in 2000–2004.

Combined wild and hatchery returns to Puget Sound (excluding ocean harvest) peaked during 1986–1988 but trended downward in the 1990s to a record low return in 1999, followed by improved returns in 2000–2003 (P. Lawson, NMFS, NW Fish. Sci. Center, 2032 SE O.S.U. Dr., Newport, OR, 97365-5275, pers. comm.). The total wild return to the Queets River on the Washington coast followed a pattern similar to that of Puget Sound, with a trend toward poor returns during 1992–1999 followed by a rebound (S. Wang, Quinault Nation, 3010 77th S.E., Suite 104, Mercer Is., WA 98040, pers. comm.). The Queets River return was exceptionally poor in 1994 and 1997 at about 2,000 fish each year but reached a peak of nearly 29,000 fish in 2001.

Wild coho salmon returns to Black Creek and Salmon River in Georgia Strait declined after 1991 and remained depressed through 2004. The Salmon River stock declined the most due to a decrease in smolt production as well as survival. Returns to Carnation Creek on the west coast of Vancouver Island declined proportionately less overall, but became highly variable during 1994–2000 with extremely low returns in 1994, 1997 and 1999.

Returns to northern British Columbia indicator systems followed relatively stable trends since the late 1980s but were very weak in 1997. Two of the northern British Columbia indicators, Lachmach River and Zolzap Creek, are located in the vicinity of the Nass River near the boundary with southeast Alaska and their pattern of abundance exhibits some features similar to nearby southeast Alaska
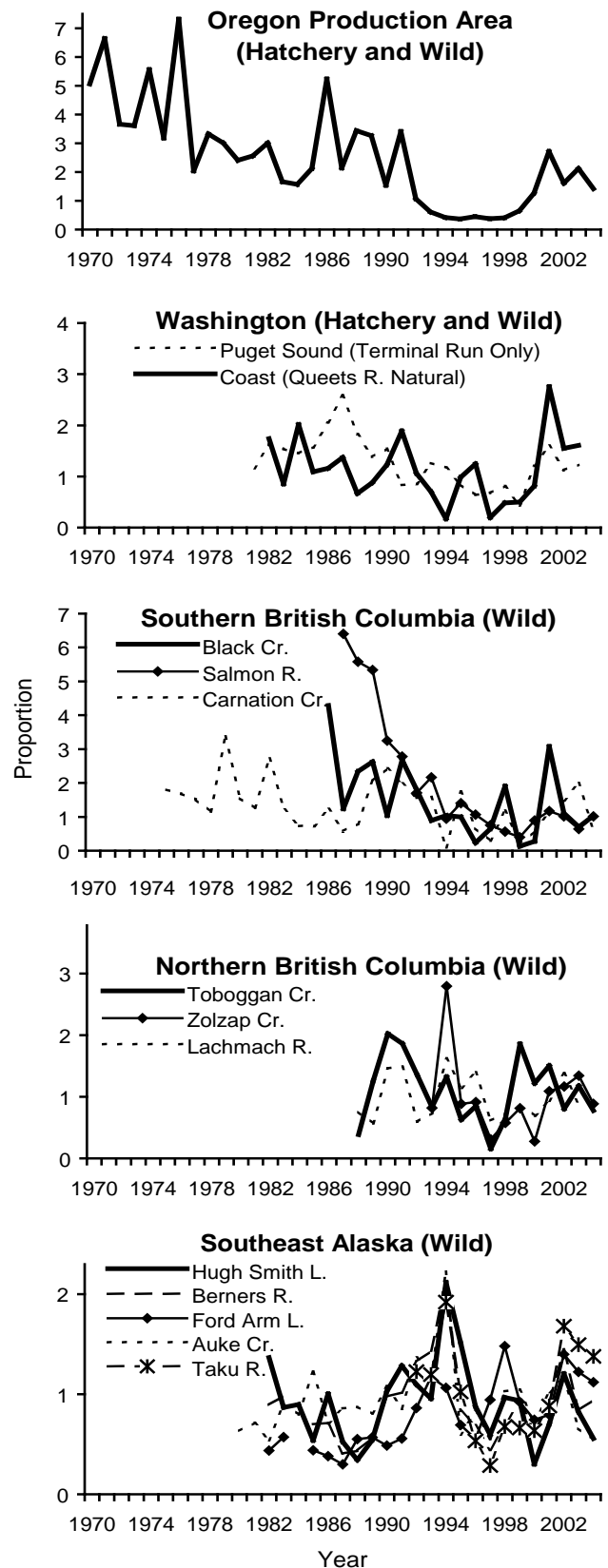

Fig. 7. Indicators of the total abundance of coho salmon returns from Oregon to southeast Alaska as a proportion of the 1993–2003 average.

stocks (Fig. 7). The return to Toboggan Creek, located further south in the upper Skeena drainage, may be more indicative of the recent abundance pattern reflected in the region's commercial catch (Fig. 3). The temporal pattern of Toboggan Creek returns compared with southeast Alaska stocks suggests that the period of highly divergent abundance indicated by commercial catch in 1992–1997 (Figs. 3 and 4) continued through 1998 before shifting again to a period of more balanced abundance between the regions.

Wild returns to most southeast Alaska systems have been relatively stable since the early 1980s, with the exception of very strong returns to inside systems in 1994 and a steadily increasing trend in returns to Ford Arm Lake, on the outer coast. Returns to the southeast Alaska indicator systems were weak on average in 2000, uniformly strong in 2002, and mixed in 2004.

ESCAPEMENT

Data series of comparable escapement estimates are very limited, particularly in more remote areas, because of the species' broad spatial distribution and tendency to spawn in coastal streams during periods of high precipitation. We examined established escapement indicators for the Oregon and Washington coasts and Puget Sound (Anonymous 2005) but restricted our review in more northern areas to limited data subsets, including only the highest quality and most comparable estimates.

Most indicators of natural coho salmon escapement from the Oregon coast to Alaska increased in 2000–2004 to levels above the averages for the 1980s and 1990s (Fig. 8). However, escapements were lower in 2004 compared with 2001–2003 in most monitored systems. In areas south of Alaska, the recent increase appears to have resulted from greatly restricted fishing combined with improved marine survival in some areas. During 2001–2004, natural stock escapements on the Oregon coast ranged from 3–5 times the 1970–1999 average.

Indicators of natural escapement also reached recent peak levels during 2000–2004 on the Washington coast, in Puget Sound and in some systems in British Columbia and Alaska. However, longer-term aggregate estimates of escapement reviewed by other authors indicate that escapements in British Columbia and the Pacific Northwest had likely decreased substantially before more detailed stock monitoring was initiated. Henderson and Graham (1998) presented information indicating that aggregate spawning escapement in British Columbia declined by over 70% from the 1950s and early 1960s to the mid-1990s.

In southeast Alaska, very little effort was made to index coho salmon escapements prior to the 1980s. Marine survival rates and fishing opportunity have remained more constant in that region. However, low fish prices during 2001–2003 led to lower exploitation rates and higher escapements for most indicator systems (Shaul et al. 2004).
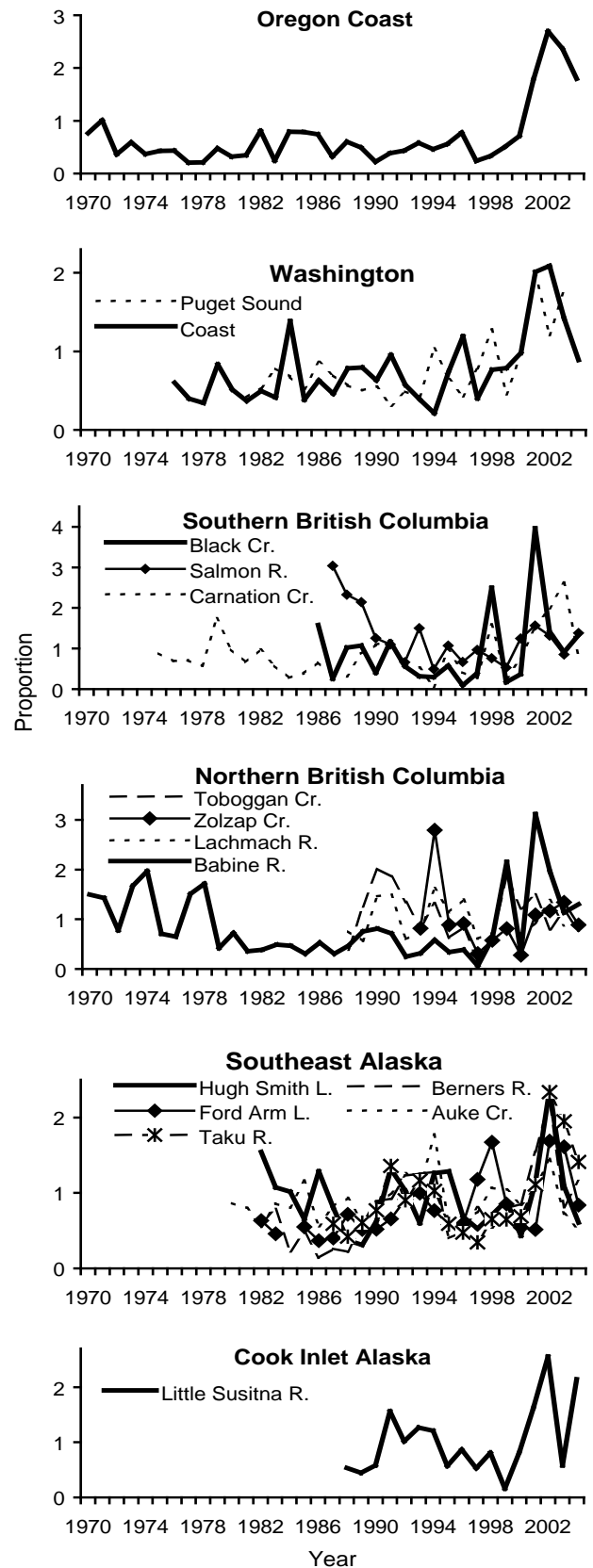

Fig. 8. Coho salmon wild indicator escapements from the Oregon coast to Cook Inlet, Alaska as a proportion of the 1993–2003 average.

MARINE SURVIVAL

Although harvest data is the only source of information indicating long-term abundance trends for most regions prior to 1975, marine survival rates provide insight into population trends and their causes during the past 20–30 years (Fig. 9). Most indicator stock projects were initiated following the 1977 regime shift, but are useful for evaluating later changes in marine survival. Hatcheries provide proxy indicators in many areas for which there are no wild stock estimates.

The number of returning adult salmon is a product of the number of smolts that migrate to sea and the proportion of those that return from the ocean to contribute to coastal fisheries and spawning escapements. A comparison of variability (coefficient of variation squared) in the number of smolts produced and their survival rate for twelve wild stocks from southeast Alaska to the Washington coast (Table 1) shows that marine survival was slightly more important on average (54%) in determining adult abundance, compared with freshwater factors including spawning escapement (46%). Spatially, the relative importance of marine survival was similar among four of the areas from southeast Alaska to Puget Sound, with its contribution to variation in adult returns being greatest for Washington coast stocks, including the Queets River (58%) and Bingham Creek (68%). However, both smolt production and marine survival were most variable, on average, for Washington and southern British Columbia stocks and least variable in southeast Alaska, with northern British Columbia being intermediate.

Marine survival varied substantially among geographical areas with wild indicator stocks in southeast Alaska and Puget Sound experiencing the highest average rates (12% or higher) and the Washington coast stocks experiencing the lowest average rates (4–6%).

Survival of smolts from inside indicator stocks in southeast Alaska peaked in the early 1990s (Fig. 9). Survival of smolts from Auke Creek in the northern part of the region increased from 9–11% in 1980–1982 to 14–25% during 1983–1989 and maintained a high average of 23% during 1990–2004. Survival rates for smolts from the Berners River in northern southeast Alaska and Hugh Smith Lake in southern southeast Alaska averaged 18% and 14%, respectively, during 1990–2004. Survival of smolts from these inside indicator stocks shows a consistent pattern over time that differs in some respects from the outer coastal stock, Ford Arm Lake. Shaul and Van Alen (2001) noted an apparent inverse relationship between average smolt production and average marine survival during 1993–1998 within two groups of closely situated systems; the first in northern southeast Alaska (Taku River, Berners River, Auke Creek) and the second in northern British Columbia and southern southeast Alaska (Nass River, Skeena River, Lachmach River, Hugh Smith Lake).

Survival rates averaged lower for wild indicator stocks in northern British Columbia, with estimates since 1990 averaging 11% for the Lachmach River and 6% for Zolzap
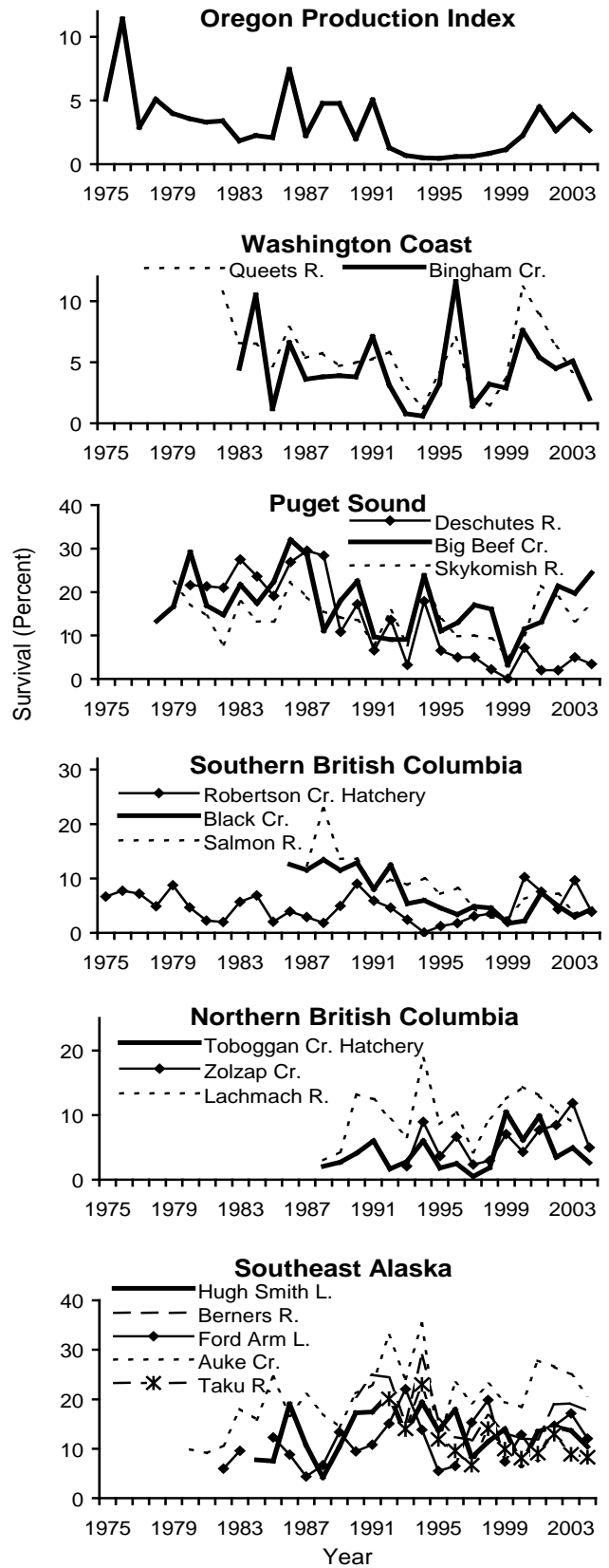

Fig. 9. Marine survival rate estimates for hatchery coho salmon smolts in the Oregon Production Index and for wild indicator stocks from Washington to southeast Alaska by adult return year.

Table 1. Average smolt production and marine survival estimates for twelve wild coho salmon stocks from southeast Alaska to the Washington coast with estimates of the percent of variation (CV^2) in total run size attributed to smolt abundance compared with marine survival.

Region	System	Return years	Average no. of smolts	Average survival (%)	Coeff. of variation		Percent of variation	
					Smolts	Survival	Smolts	Survival
Southeast Alaska	Auke Cr.	1980–2004	6,369	20.3	0.26	0.33	39	61
	Berners R.	1990–2004	201,857	17.6	0.29	0.30	47	53
	Hugh Smith L.	1984–2004	31,160	12.9	0.30	0.36	42	58
	Taku R.	1992–2004	1,592,808	12.0	0.46	0.40	56	44
N. British Columbia	Lachmach R.	1988–2003	31,324	10.0	0.43	0.42	52	48
	Zolzap Cr. [1]	1993–2004	63,201	5.9	0.53	0.51	51	49
S. British Columbia	Black Cr.	1986–2004	60,770	7.1	0.58	0.57	51	49
	Salmon R.	1987–2004	125,694	8.5	0.48	0.58	41	59
Puget Sound	Big Beef Cr. [2]	1979–2003	25,165	17.2	0.38	0.40	47	53
	Deschutes R. [2]	1980–2004	54,632	13.1	0.76	0.76	50	50
Washington Coast	Queets R. [3]	1982–2003	222,637	5.5	0.41	0.47	42	58
	Bingham Cr. [2]	1983–2004	32,053	4.4	0.45	0.66	32	68
				Average	0.44	0.48	46	54

[1] Bruce Baxter, LGL Ltd., 9768 2nd St., Sidney, BC, Canada V8L 3Y8, personal communication.

[2] Greg Volkhardt, Wash. Dept. of Fish and Wildlife, Science Div., Olympia, WA 98501, personal communication.

[3] Shizhen Wang, Quinault Nation, 3010 77th S.E., Suite 104, Mercer Is., WA 98040, personal communication.

Creek (B. Baxter, LGL Ltd, 9768 2nd St., Sidney, BC, Canada V8L 3Y8, pers. comm.). Survival rates for these stocks showed substantial fluctuation but no clear trend during this period. Both systems are in the far northern portion of the British Columbia coast and may not be reflective of marine survival further south from the Skeena River to Cape Caution, or in the Queen Charlotte Islands. Survival rates for smolts released from the Toboggan Creek Hatchery in the upper Skeena River system averaged 4% for 1988–2004 returns, including a very low survival rate of 0.5% in 1997 that corresponded with a record low commercial harvest in northern British Columbia. Survival of Toboggan Creek smolts increased dramatically in 1999–2001 after a period of generally poor survival in 1992–1998.

Average survival rates for hatchery stocks in British Columbia declined substantially after the 1981 return and continued to decline after the mid-1980s (Coronado and Hilborn 1998). The decline in the latter period is evident in survival rates of wild indicator stocks in Georgia Strait, which decreased from an average of 10% for Black Creek and 12% for Salmon River in 1986–1994 to average rates of 4% and 5%, respectively, during 1995–2004. Marine survival of smolts from Robertson Creek Hatchery on the west coast of Vancouver Island has been highly variable in recent years,

ranging from barely more than 0% (1994) to 10% (2000) with a long-term average of 5%. Robertson Creek survival rates averaged just over 7% during 2000–2004, similar to the earliest years on record (1975–1977).

Survival rates have been highly variable for Pacific Northwest stocks. Two of the long-term indicator stocks located in mid-Puget Sound, Big Beef Creek and Skykomish River, appeared less affected by ocean conditions that resulted in reduced survival of many other Pacific Northwest and southern British Columbia stocks during the mid-1990s. Survival rates during 1992–1999 averaged 13% for Big Beef Creek and 11% for the Skykomish River, down from 20% and 16%, respectively, in 1978–1989 (P. Lawson, NMFS, NW Fish. Sci. Center, 2032 SE O.S.U. Dr., Newport, OR 97365-5275, pers. comm.). Survival rates for those stocks were high at 24% in 1994, a year when survival rates for stocks on the outer coast from Oregon to southern British Columbia were at or near record lows. In contrast with the two mid-Puget Sound stocks that have rebounded, marine survival of smolts from the Deschutes River located in southern Puget Sound has trended lower since 1995 (Fig. 9).

Survival of Washington coast indicator stocks declined sharply from a relatively steady trend averaging 5–6% in

1982–1992 to very low marine survival rates of 1–3% in 1993–1994 for the Queets River on the Olympic Peninsula and under 1% for Bingham Creek in Grays Harbor. Survival of these stocks then increased to 7% and 12%, respectively, in 1996 before declining again to between 1% and 4% in 1998 and 1999.

Hatchery smolts in the Oregon Production Index (OPI) followed a similar survival pattern to Washington coast stocks during the 1990s, but with the notable absence of a rebound during 1995–1997. OPI survival rates declined sharply beginning in 1992 from a 1975–1991 average of about 4.2% and remained at rates of 0.5–1.3% during 1992–1999 before rebounding to an average rate of 3.2% during 2000–2004.

SIZE AT TIME OF RETURN

A number of authors have noted a decreasing trend in the size of adult coho salmon, particularly in the southeastern part of their range (Ricker and Wickett 1980; Ricker 1981, 1995; Bigler et al. 1996). Weitkamp et al. (1995) reported a significant negative slope in 20 out of 35 time series of average weight and length measurements in coho salmon from California to southern British Columbia. They reported that adult coho salmon in Puget Sound and the Strait of Georgia declined at a much faster rate than in other areas, with Puget Sound fish declining by about 50% from 1972 to 1993.

We examined the average weight of fish caught in the troll fishery off the west coast of Vancouver Island (WCVI) and in net fisheries of the lower Columbia River in Zones 1–5 (Anonymous 2002b; S. Engwall, Oregon Dept. of Fish and Wildlife, 17330 SE Evelyn St., Clackamas, OR 97015, pers. comm.). Both data sets show a linear decline from the 1950s through the early 1990s (Fig. 10). The average weight of Columbia River fish declined from 1957 to 1992 (slope = -0.035; $p < 0.001$). The trend then abruptly reversed, and average weight rebounded at a faster rate during 1993–2004 (slope = 0.082; $p < 0.001$). The mean-average weight of 4.13 kg in 2000–2004 was actually higher than the average of 4.00 kg in the first five years of the data series (1957–1961) and was 43% above the lowest five-year mean-average weight of 2.89 kg in 1989–1993.

Coho salmon size in southern British Columbia followed a similar pattern, based on the average weight of fish landed in the WCVI troll fishery in Area 23 in September and sampled in escapements of two Vancouver Island systems. The data series for the troll fishery adds an additional 20 years of average weights to comparable 1951–1975 figures reported by Ricker and Wickett (1980). The average weight of coho salmon landed in the WCVI troll fishery declined by about 60% from 1951–1992 (slope = -0.050; $p < 0.001$). The fishery was closed after 1995.

In order to evaluate more recent trends in average weight of coho salmon in southern British Columbia, we converted average fork length to round weight for spawners from two wild stocks in southern British Columbia using a
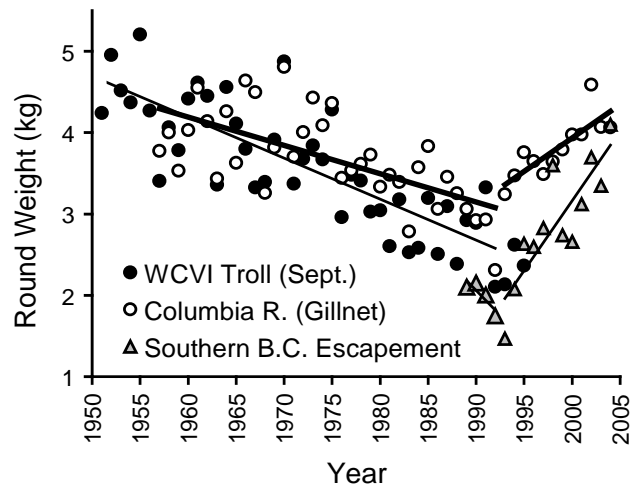
Fig. 10. Average round weight of coho salmon caught in the troll fishery on the west coast of Vancouver Island (WCVI) during September and the Columbia River gillnet fishery, and the mean-average weight of adult coho salmon in escapements to Black and Carnation creeks in southern British Columbia. Linear trends are shown for periods ending in 1992 and beginning in 1993.
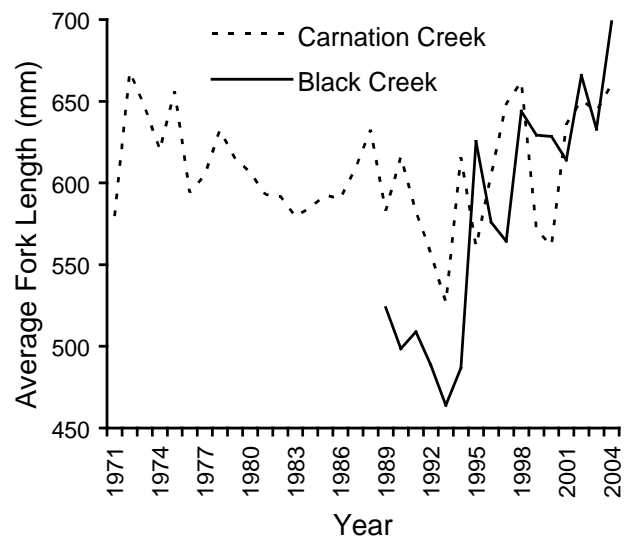
Fig. 11. Average mid-eye to fork length of age .1 wild adult coho salmon spawners in Carnation Creek on the outher coast of Vancouver Island and Black Creek on the east (Georgia Strait) side of Vancouver Island.

conversion estimate developed by Gray et al. (1981). Note that this conversion imposes the assumption that body condition remains constant, so converted weights may be a less sensitive indicator than actual measured weight. Trends in mean-average weight (kg) converted from length for the two stocks, Carnation Creek and Black Creek (Fig. 10), show an increase during 1993–2004 (slope = 0.172; $p < 0.001$). The estimated mean-average weight of spawners in the two creeks increased by 57%, from 1.91 kg in 1989–1993 to 2.99
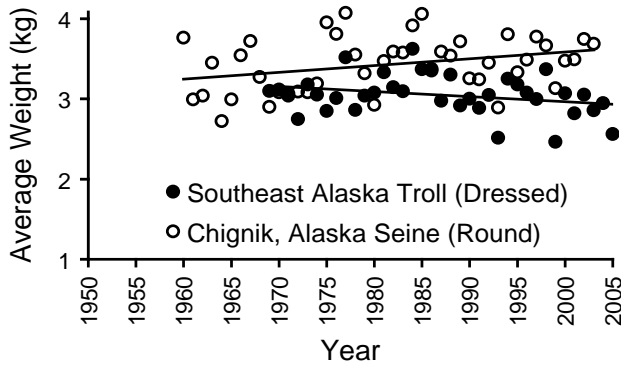
Fig. 12. Average weight of coho salmon caught in the southeast Alaska troll fishery (dressed weight) and in the Chignik purse seine fishery on the Alaska Peninsula (round weight).

kg in 2000–2004. The average length of spawners showed a far more marked increase since 1993 at Black Creek in the Strait of Georgia compared with Carnation Creek on the outer coast (Fig. 11) suggesting that the factors responsible for the decline in size were more influential in inside waters. Stocks in Georgia Strait and Puget Sound experienced the steepest decline in size prior to 1993 (Weitkamp et al. 1995).

It is unclear to what extent the decline and rebound in size of coho salmon in the Columbia River and southern British Columbia can be attributed to changes in fishing practices, changes in ocean productivity, density-dependent effects related to hatchery releases, or a combination of factors. Fisheries were conducted relatively consistently during the period of decline and were greatly curtailed in the early to mid-1990s, at about the time of the reversal. At least two broadly recognized ocean regime shifts occurred during the period and fish were large, on average, prior to 1978 when ocean conditions were most favorable for marine survival. However, size has rebounded to near pre-1978 levels, while recent hatchery smolt survival rates in the Oregon Production Index averaged only about half of survival rates prior to 1978. For both fisheries, we found weight to be negatively correlated with the number of fish released from hatcheries in the prior year. Average weight of Columbia River fish in 1960–2003 was negatively correlated with releases from facilities on the Columbia River and Oregon and Washington coasts (R^2 = 0.43; slope = -0.020; p < 0.001) while average weight in the WCVI troll fishery during 1960–1995 was negatively correlated with releases from facilities in southern British Columbia, Puget Sound and the Washington coast (R^2 = 0.59; slope = -0.022; p < 0.001). These relationships suggest that the increase and decline in hatchery production could have been an important factor contributing to trends in fish size.

In contrast to the Pacific Northwest and southern British Columbia, we detected very little change in the size of coho salmon landed in Alaskan fisheries, including two represen-

tative fisheries in the eastern and western Gulf of Alaska involving a single, relatively non-selective gear type (Fig. 12). There was no significant trend in average weight of coho salmon landed in the southeast Alaska troll fishery during 1969–2005 (slope = -0.004; p = 0.29) and a slight increasing trend in weight of fish landed in the Chignik purse seine fishery on the Alaska Peninsula during 1960–2003 (slope = 0.008; p = 0.03).

DISCUSSION

Although the overall Pacific Rim catch has remained near record low levels since the mid-1990s, other recent information on the status of wild stocks is more positive. Overall Alaskan production appears to have remained near the high levels experienced beginning in the early 1980s while spawning escapements have improved in most areas from British Columbia southward as a result of reduced fishing since the mid-1990s, combined with improved marine survival for some systems since 1999. A recent rebound in average adult weight in southern populations has alleviated concerns about the effect of decreasing size on spawning success (Weitkamp et al. 1995). Over the longer term, however, we anticipate that natural production of this species, particularly in the southern portions of its range, will continue to be challenged by freshwater environmental change brought about by increasing human development and climate change. Populations at lower latitudes will likely continue to experience greater variability in both smolt production and marine survival compared with southeast Alaska populations. Recent declines in hatchery production combined with environmental and management changes make it unlikely that the Pacific-wide commercial catch will rebound to levels in the mid-1960s to mid-1990s that routinely exceeded 10 million fish annually.

Smolt production and marine survival estimates from throughout the coast indicate that freshwater and marine environments have both had an important influence on adult coho salmon returns, with marine survival contributing slightly more on average to variability in abundance within the past 25 years. Within the marine survival component, major differences in the spatial and temporal pattern of survival indicate that conditions specific to very localized marine waters such as southern Puget Sound can have a critical influence on abundance. At the same time, consistent decadal-scale patterns exist among major geographical areas such as southeast Alaska and northern British Columbia, and with other species, including pink salmon.

Evident trends in the average size of coho salmon raise interesting questions that deserve further study. Why have Alaskan adults not declined in size in conjunction with a tremendous increase in the number of salmon returning to the state? Why did fish in more southern areas decrease in size for about three decades, followed by a rapid rebound since 1993?

Changes in exploitation by selective fishing gear, density dependence related to changing hatchery production, and shifts in ocean productivity have all been suggested as potential explanations for the decline in size in southern areas (Weitkamp et al. 1995). The rapid rebound in size suggests that selective harvest, to the extent that it may have been responsible, did not have a lasting genetic effect on fish size. Substantial differences between inside stocks and coastal stocks, and an inverse relationship between adult size and hatchery production, both point toward potential limitations in productivity in local marine waters. On the other hand, a similar size decline in other salmon species in the North Pacific (Bigler et al. 1996) and an apparent reversal in a declining trend in chum salmon size in Washington and southeast Alaska in the mid-1990s (Helle and Hoffman 1998) suggest that the factors responsible for recent trends in adult size in southern coho salmon stocks may also be linked to broad change across the North Pacific ecosystem.

In some respects, the coho salmon is a difficult species to assess for historical abundance. Catches are minimally informative through time over most of its range because of changes in habitat capacity, artificial culture, markets and fishing regulations, and reliable escapement information is limited or non-existent in some regions. On the other hand, the species is very conducive to informative high-resolution research on an individual population basis. Specific life-history aspects, including relatively stable size at sea-entry and a stable ocean age, make it a consistently useful indicator species for marine conditions affecting both survival and growth. Wild indicator stocks from southeast Alaska to Washington not only provide information on the relationship between spawning escapement and population abundance needed for informed fishery management (Bradford et al. 2000), they also provide critical support for the role of coho salmon as a valuable indicator species for environmental change in freshwater and ocean environments. Continuation of these programs is essential in order for the species to fill both important roles.

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Diets of Pacific Salmon in the Sea of Okhotsk, Bering Sea, and Northwest Pacific Ocean

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Abstract: Since the 1950s the food habits of Pacific salmon have been studied from samples representing multiple salmon life-history stages, collected from principal feeding areas (Sea of Okhotsk, Bering Sea, and Northwest Pacific Ocean) within Russia's 200-mile economic zone. Data have been gathered by various types of fishing gear designed to catch juvenile and adult salmon. Using a comparative analysis, we examined feeding habits of pink, chum and sockeye salmon. Our results showed that in the 1950s, in offshore waters, the principal prey of these salmon consisted of energetically valued hyperiids and euphausiids. The basic juvenile salmon diet consisted of copepods, which also contributed substantially to the food of returning adults. Diets were stable until the 1980s, when the contribution of pteropods and juvenile fish to salmon diets became more significant. Since that time, low-energy organisms, including arrow worms, appendicularia, and salps, have appeared in the diets of salmon in relatively high numbers, particularly in the Bering Sea. Chum salmon have the most varied diet, and may be the best indicator of plankton production. Research shows that changes in diet can be associated with changes in plankton and nekton abundance. Regional variables and salmon abundance have also affected salmon diet composition. The composition of salmon diets has affected the size and average age at maturity toward the end of the last century, which has influenced the productivity of salmon stocks and populations.

Keywords: salmon, food spectrum, variability, food similarity, component, survival, production

INTRODUCTION

Trophic interactions are one of the key factors determining not only the biological characteristics of fish, but also their survival which, in turn, regulates salmon abundance and productivity. The state of the salmon forage base depends on oceanic climate conditions that influence the development of the principal components of zooplankton and nekton in areas where salmon migrate during particular periods in their life cycle. Further, salmon migrations are seasonal, which also influences their food supply and, therefore, the survival of generations.

These interactive processes cannot be explained based on episodic or short-term observations, especially if such observations are based only on a particular unit of a fish stock. Proper analysis requires continuous observations using a common method to create a large database for comparison. Data on Pacific salmon in most regions of the North Pacific Ocean have been collected by KamchatNIRO (since the mid 1950s) and by TINRO-Centre (since the mid 1980s).

The purpose of this paper is to examine and analyze the content, weight, and prey composition by stomach analysis of pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and

sockeye (*O. nerka*) salmon during different periods of oceanic life to assess of the influence of trophic interactions on the development of biological parameters and the abundance of salmon in the Northwest Pacific Ocean.

MATERIALS AND METHODS

Archival materials and published long-term datasets, collected by researchers from Russian research institutions, primarily KamchatNIRO, for the first decades of Pacific salmon studies were used for our analyses (Andriyevskaya 1957, 1958, 1964). This period, beginning with the studies of adult salmon at KamchatNIRO, covers over 50 years (from 1954), and for juvenile salmon, about 40 years (from 1965) (Karpenko 2003). Unfortunately, there is no continuous line of observation for any particular area or for any one species. Also, there is no standard method for collecting and processing data because the methodologies have either changed or improved over time. Most of the changes are related to modernization of vessels and techniques for sampling and processing. All data used in this analysis were transformed into a standard format and processed with the same methods. Individual weight measurements for over

10,000 adult salmon and over 14,000 juveniles were available. The data from the BASIS program have also been analyzed (Volkov et al. 2005). That analysis included 11,671 stomachs of three species: pink salmon (2,119 specimens), chum (5,617 specimens) and sockeye (3,935 specimens), which were collected throughout the Bering Sea. Our current analysis uses the results of studies of 1,592 juveniles and 3,861 maturing salmon, caught only in the western Bering Sea. We examined 10,000 stomachs of each of the species mentioned. Additionally we used data from the published literature about the feeding habits of these species in particular areas of the Far Eastern seas, and adult salmon biological parameters and abundance.

RESULTS AND DISCUSSION

Juvenile Pacific Salmon Diets

The river systems (rivers and lakes) flowing into the Sea of Okhotsk provide spawning areas for all species of Asian Pacific salmon, except chinook. The Sea of Okhotsk is the most important feeding area for juvenile Pacific salmon stocks of Asian origin. In spring, salmon emerge from the rivers and begin feeding in coastal waters, mixing extensively before leaving for the high seas of the North Pacific. The diet of juvenile pink, chum and sockeye salmon consists of approximately 60 species: over 50 species in the diet of pinks, 45 in the chum diet, and 35 in the sockeye diet.

In the Sea of Okhotsk the most abundant species is the juvenile pink salmon, although in some years chum salmon can dominate. The dominance of chum salmon occurred most often in the 1960s and 1970s, two decades of very reduced salmon abundance. Juvenile pink salmon, perhaps because of its abundance and its early and rapid migration to the Okhotsk Sea, has the widest spectrum of food of all the species of salmon. The basic diet consists of hyperiids, euphausiids, copepods, and pteropods. The summary percentage of these organisms is usually over 80% of the total food weight. During all of the years of observation, hyperiids played a dominant role, providing 29 to 67% of food weight (Fig. 1A). In the 1960s and 1970s this taxon dominated at 67 and 51%, respectively, whereas in the 1980s, 1990s and 2000s it made up about one-third of the diet of juvenile pink salmon (ranging from 29% to 35%). The dominant species was *Themisto japonica*. Only in 1969 did another species, *T. libellula*, supply the bulk of food (86%). In the 1960s the second most dominant food source were copepods (13%). The percent of all of the other food components did not exceed 5% of food weight. In the 1970s and 1980s, besides a high percentage of hyperiids, pink salmon also consumed euphausiids (18% and 11%, respectively) and copepods (11% and 18%, respectively). In the 1990s and 2000s, pteropods (22% and 26%, respectively), copepods (16% and 14%, respectively) and euphausiids (12% and 23%, respectively) made up a significant percentage of food weight. Only in the 1970s did

juvenile fish provide over 8% of food weight; in the other periods the percentage was lower. A narrow food spectrum for pink salmon was recorded in the 1960s and 1970s (16 and 13 components, respectively). A wide spectrum was seen in the 1990s and 2000s (30 and 24 components, respectively). Average stomach fullness varied extensively, from 56.3 to $312.9^{\circ}/_{\circ\circ\circ}$. It was highest in the 1980s (up to $313^{\circ}/_{\circ\circ\circ}$), and lowest by the late 1990s and into the 2000s (< $200^{\circ}/_{\circ\circ\circ}$). Overall, the dominance of hyperiids in the diet was observed in years of low pink salmon abundance, whereas a high percent of pteropods, copepods and euphausiids was observed in years of high pink salmon abundance.

Chum salmon also consumed mostly hyperiids, contributing 22–64% of food weight (Fig. 1B). Similar to pink salmon, *T. japonica* formed the basis of the juvenile chum salmon diet; *T. libellula* dominated (90.5%) only in 1969. In addition to these species, in the 1960s and 1970s chum salmon consumed juvenile fish (9% and 14%, respectively) and euphausiids (9% and 16%, respectively). In the 1980s and 1990s, chum salmon consumed *Oikopleura* sp. (20% and 26%, respectively) and pteropods (12% and 22%, respectively). In recent years the chum salmon diet included a significant percentage of euphausiids (24%), pteropods (16%), copepods (11%) and *Oikopleura* sp. (10%). A narrow food spectrum (up to 16 components), similar to the spectrum of the pink salmon diet, was observed in chum salmon in the 1960s and 1970s, and a wide spectrum (up to 25 components) in the 1990s and 2000s. The stomach fullness of chum salmon was lower ($34–220^{\circ}/_{\circ\circ\circ}$) compared to values for pink salmon. It was also high in the 1980s (54 to $220^{\circ}/_{\circ\circ\circ}$), and low (up to $130^{\circ}/_{\circ\circ\circ}$) in the 1960s and recent 2000s. In general, the percentage of hyperiids decreased from 64 to 27%, whereas the percentage of euphausiids increased (to 24%), as well as pteropods (to 22%), *Oikopleura* sp. (to 26%), and copepods (to 11%).

Sockeye salmon have the most narrow food spectrum of all Pacific salmon. In the 1960s, 1970s and 1980s they fed mostly on hyperiids (43%, 48% and 35% of food weight, respectively) (Fig. 1C). Among other plankton, only juvenile fish (34% in the 1960s) and euphausiids (18% in the 1970s, and 20% in the 1980s) played an important role in sockeye diets. During this period (1960s to 1980s) the sockeye food spectrum included only 5–11 components. In the 1990s and 2000s the food spectrum of juvenile sockeye increased to up to 20 components, and an important role was played by pteropods (30% in the 1990s, and 15% in the 2000s) and euphausiids (15% in the 1990s, and 28% in 2000s). Besides these taxa others began to play more important roles, including juvenile fish (14% in the 1990s, and 19% in the 2000s), copepods (16% in the 2000s), larval crabs (8% in the 1990s, and 10% in the 2000s), among others. The stomach fullness of juvenile sockeye was lower, when compared with other species, and did not exceed $100^{\circ}/_{\circ\circ\circ}$ (varying from 18 to $98^{\circ}/_{\circ\circ\circ}$). During the periods of observation it varied little, showing little evidence of food sustainability for this salmon species.
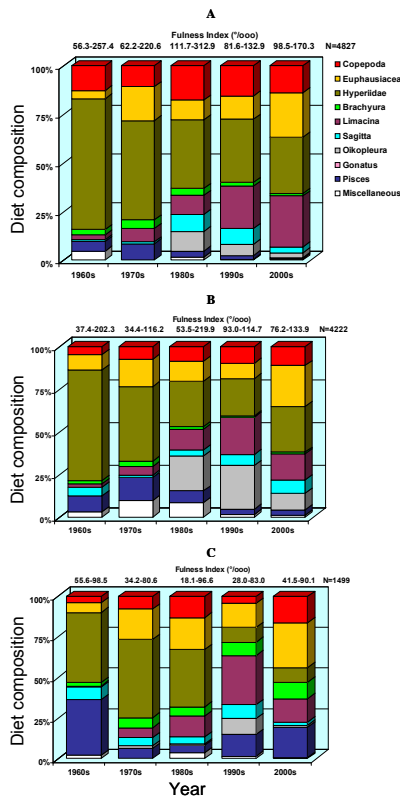
Fig. 1. Diet composition of juvenile pink (A), chum (B) and sockeye (C) salmon (1960s–2000s) in the Okhotsk Sea.

Fig. 2. Diet composition of juvenile pink (A), chum (B) and sockeye (C) salmon (1960s–2000s) in the Bering Sea. Key as in Figure 1.

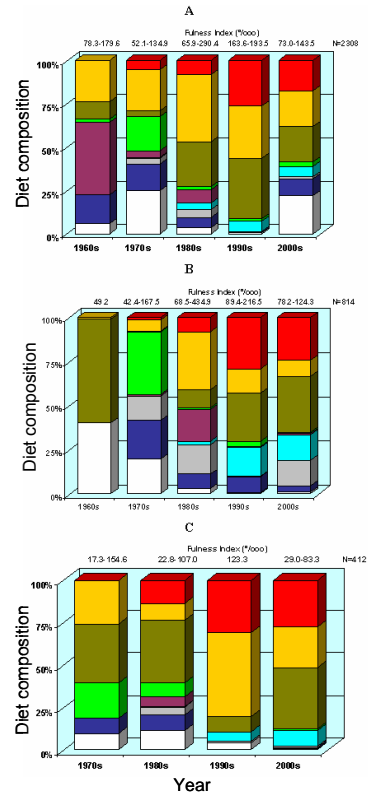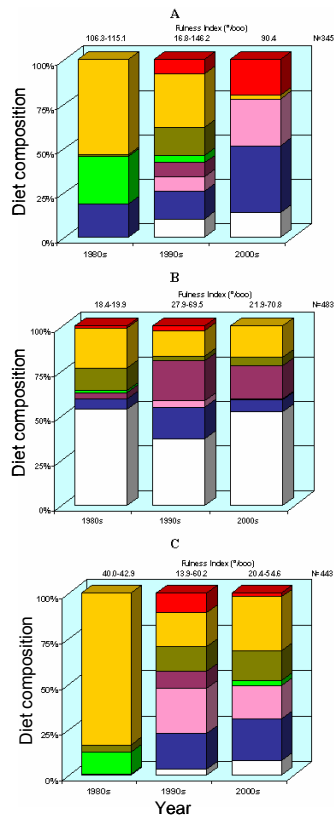**Fig. 3.** Diet composition of adult pink (A), chum (B) and sockeye (C) salmon (1980s–2000s) in the Bering Sea. Key as in Figure 1.
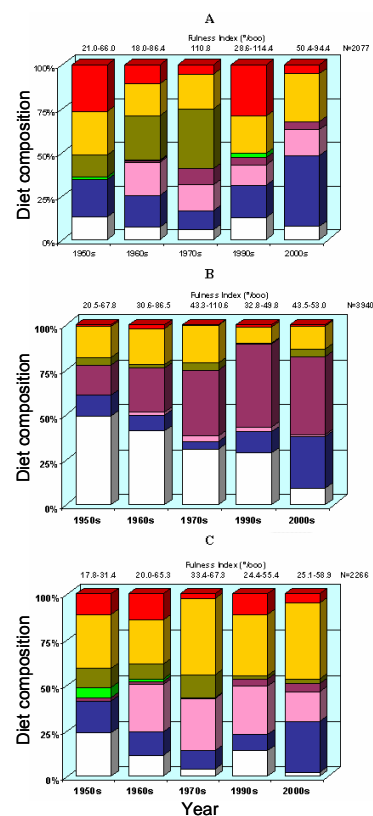

Fig. 4. Diet composition of adult pink (A), chum (B) and sockeye (C) salmon (1950s–2000s) in the Northwest Pacific Ocean. Key as in Figure 1.

Among the three species of juvenile Pacific salmon in the Sea of Okhotsk the most consistent consumer of marine crustaceans is the sockeye salmon. Pink salmon also prefer high caloric crustaceans, including hyperiids, euphausiids and copepods (Yerokhin and Shershneva 2000; Shershneva and Koval 2004). Chum salmon consume a varied diet with a wide spectrum of food. When pink salmon are abundant, they consume a larger number of organisms of lower caloric value, including pteropods and *Oikopleura* sp., among others.

In the western Bering Sea, juvenile salmon have a relatively narrow food spectrum, compared to those in the Sea of Okhotsk, and consisting of < 50 components. The diet of juvenile pink salmon includes 43 components, chum salmon includes 39, and sockeye salmon includes 28. The main diets of juvenile sockeye consisted of euphausiids, hyperiids and copepods, and also larval crabs and juvenile fish. Occasionally other plankton began to play an important or even dominant role.

For example, in the 1960s the principal food of juvenile pink salmon were pteropods (42% of food weight). Other plankton were less important, including euphausiids (24%), juvenile fish (17%) and hyperiids (10%) (Fig. 2A). In the 1970s, the most numerous items were euphausiids (24%), *Podon* sp. (21%), larval crabs (20%) and juvenile fish (15%). A more stable but wider food spectrum was observed in juvenile pink salmon during the 1980s and 2000s, when the principal food consisted of crustaceans, including euphausiids (26–39% of food weight), hyperiids (26–35%) and copepods (8–26%). The principal species of Copepoda were *Neocalanus cristatus* and *N. plumchrus*, although in 1990 *Eucalanus bungii* made up 20% of the food weight. The percentage of other organisms was very low: in the 1980s pteropods made up 8% of food weight, and in the 2000s juvenile fish made up 13%. During the periods of observation from 1965 to 2002 the juvenile pink salmon food spectrum increased from 3 to 28 components. The spectrum was the narrowest during the period of low catches in the 1960s and 1970s (3–11 components). However, the stomach fullness was highest in the 1960s (from 78–180$^{\circ}/_{ooo}$) and in the 1980s (66–290$^{\circ}/_{ooo}$). The stomach fullness of pink salmon was low in the 1970s (52–135$^{\circ}/_{ooo}$) and 2000s (73–144$^{\circ}/_{ooo}$).

The food spectrum of juvenile chum salmon showed the widest seasonal and interannual variations (Fig. 2B). For example, in 1965 the basis of the chum salmon diet consisted of hyperiids (59%) and *Polychaetae* (31%). In the 1970s it consisted of larval crabs (35%) and juvenile fish (22%), and in the 1980s it consisted of euphausiids (33%), pteropods (18%) and *Oikopleura* sp. (17%). In 1978 *Oikopleura* sp. accounted for 30% of food weight. Only in the 1990s and 2000s did crustaceans (including hyperiids (27-31%), copepods (24–29%) and euphausiids (9–14%)) play an important role in chum salmon diets; the role of arrow worms was also important (15% to 16%). In the course of our studies the chum salmon food spectrum increased from 5 to 22 com-

ponents. Low stomach fullness (42–168$^{\circ}/_{ooo}$) was observed from 1965 to 1970, and in the 2000s (78–124$^{\circ}/_{ooo}$). It was the highest (up to 434$^{\circ}/_{ooo}$) in the 1980s.

Juvenile sockeye had the most consistent food spectrum, consisting of crustaceans, including hyperiids, euphausiids and copepods, that varied by year (Fig. 2C). During the 1970s, 1980s and 2000s hyperiids dominated, making up > 35% of the food weight. Only in the 1990s did this group fall to third place behind euphausiids (49%) and copepods (31%). Among the other plankton only larval crabs in the 1970s (21%) and juvenile squid in the 1980s (11%) played an important role in the sockeye diet. The number of food components varied from 3 to 14 in those decades. The stomach fullness of juvenile sockeye was also relatively stable, varying from 17 to 155$^{\circ}/_{ooo}$, with an average of approximately 100$^{\circ}/_{ooo}$. These characteristics suggest that sockeye salmon are the most consistent consumer of crustaceans in the western Bering Sea.

Adult Pacific Salmon Diets

The food spectrum of adult salmon was different from that of juveniles. It was significantly wider, consisting of approximately 60 components: 34 components in pink, 45 in chum, and 43 in sockeye salmon. The role of crustaceans was significant only in the spectrum of pink and sockeye salmon, while chum were feeding mostly on other organisms.

The diet of adult pink salmon in the 1980s and 1990s consisted of euphausiids (54% and 30%, respectively) (Fig. 3A). In the 1980s, besides these organisms, there was a high percentage of larval crabs (27%) and juvenile fish (19%), and in the 1990s there was a high percentage of hyperiids and juvenile fish (16% for each). Juvenile fish was the basis of the adult pink salmon diet in the 2000s (38%), when other items in the diet consisted of juvenile squid (26%) and copepods (20%). The average stomach fullness varied by year and was about 100$^{\circ}/_{ooo}$.

Chum salmon consumed mostly euphausiids (14–22%), pteropods (4–22%) and juvenile fish (6–18%) (Fig. 3B). However, usually up to one-third of the chum salmon diet was difficult to identify because the prey items were rapidly digested. Among crustaceans only euphausiids made up a significant part of the food spectrum (14–22%), while hyperiids and copepods rarely contributed more than 10% of food weight. The stomach fullness of chum salmon usually was low, not over 70$^{\circ}/_{ooo}$, but the food spectrum was relatively wide in the 1980s, consisting of 24 components.

The sockeye salmon diet in the 1980s and 2000s consisted of euphausiids, which made up 84% and 30%, respectively, of the food weight (Fig. 3C). Besides these groups in the 2000s, there was a significant percentage of juvenile fish (23%), squid (18%) and hyperiids (16%). The widest spectrum of food (23 components) was recorded for sockeye adults in the 1990s, when the principal food items were

juvenile squid (25%) and fish (20%), and also euphausiids (19%), hyperiids (14%) and copepods (11%). The stomach fullness of sockeye salmon was the lowest among all salmon and never exceeding $60°/_{ooo}$, and averaging slightly $> 40°/_{ooo}$.

In the western Bering Sea the principal food of both adult and juvenile salmon,was crustaceans, including euphausiids, hyperiids and copepods. Occurrence of other food components was recorded in the cases of increased abundance of consumers or transformations in pelagic plankton or nekton communities when salmon began to consume large amounts of pteropods, juvenile fish and squid, as well as *Chaetognatha* and *Oikopleura* spp. Among three salmon species – pink, chum and sockeye, sockeye salmon had the least variable diet. Chum had the most variable diet. Pink salmon took an intermediate position. However, because of the high abundance of pink salmon, they influence the state of pelagic crustacean communities, which may determine the interannual variations in productivity of particular salmon species.

In the Pacific Ocean waters off Kamchatka the adult salmon returning to spawn in the river systems of the Far East are caught by gillnets. Kapron nets were used until the 1970s, and were later replaced by fibre nets. These nets undoubtedly have different fishing efficiencies. Kapron nets were used mostly for research purposes until the 1980s. The fibre nets were used in the Japanese Pacific salmon fishery, and also for the last ten years on Russian research vessels.

The food composition of salmon diets included approximately 70 components. Chum had the widest food spectrum (69 components), with sockeye having the narrowest spectrum (52 components). Pink salmon had an intermediate position (58 components). The wider food spectrum of chum salmon, compared to the other salmon species, is determined by a larger contribution and number of jelly-bodied organisms and juvenile fish.

Pink salmon adults consumed mostly crustaceans - copepods, hyperiids and euphausiids, and also pteropods, squid and juvenile fish; the percentage of these components showed significant interannual variations (Fig. 4A). In the 1950s the principal components of pink adult diets were: copepods (27%), euphausiids (25%) and juvenile fish (21%); in the 1960s they were hyperiids (24%), juvenile squid (19%) and fish (18%); in the 1970s, hyperiids (34%), euphausiids (20%) and juvenile squid (15%); in the 1990s, copepods (30%), euphausiids (21%) and juvenile fish (19%); and in the 2000s, juvenile fish (40%), euphausiids (28%) and juvenile squid (15%). In some years the basic diet consisted of relatively rare plankton species. For example, *Sagitta elegans* in February–April in 1986 made up 33–45% of the food weight, and squid in 1962 made up 62.6% and in 2000, made up 40.3%. The widest food spectrum (23 components) was shown in pink salmon adults in the mid 1950s and early 2000s; the narrowest spectrum was seen in the early 1960s (8 components). The stomach fullness was relatively low in the 1950s and 1960s ($18–86°/_{ooo}$) and relatively high in the 1970s. The increase in recent years (over $100°/_{ooo}$), is perhaps

due to the use of different gillnets. Overall, the dominance of juvenile fish and squid in diets was observed during years of high abundance of pink salmon, whereas the dominance of crustaceans was recorded in years of low abundance of pink salmon.

Chum salmon fed mostly on pteropods, euphausiids and juvenile fish, and sometimes a high percentage of coelenterates (Fig. 4B). The latter dominated (21%) in the 1950s, in particular in 1957 when they made up 72.6%, in 1958 when they made up 49.6% and in 1997 when they made up 27.8% of food weight. Chum salmon also fed on euphausiids (17%) and juvenile fish (12%). In the 1960s the basis of the adult chum diet consisted of pteropods (25%) and euphausiids (20%); in the 1970s, 1990s and 2000s it consisted of pteropods (37–46%), euphausiids (9–21%) and juvenile fish (5–29%). The widest food spectrum (30 components) was shown in adult chum diets, similar to that for pink salmon in the mid 1950s and early 2000s. The narrowest spectrum for adult chum was seen in the mid 1960s and early 1970s. Stomach fullness of adult chum salmon was always lower in comparison to that of the other salmon, and only in the 1970s was it over $100°/_{ooo}$. Similar to pink salmon, chum salmon showed a dominance of pteropods and juvenile fish in diets during high salmon abundance, in particular pink salmon.

Sockeye salmon consumed mostly euphausiids, juvenile squid and fish, with a lesser role played by copepods, hyperiids and pteropods (Fig. 4C). In the 1950s the principal components in sockeye diets were euphausiids (30%), juvenile fish (17%), copepods (11%) and hyperiids (11%); in the 1960s the principal components were juvenile squid (26%), fish (13%), euphausiids (25%) and copepods (15%); in the 1970s and 1990s euphausiids (42% and 34%, respectively) and juvenile squid (29% and 27%, respectively) were most important; in the 2000s, euphausiids and juvenile squid (41% and 16%, respectively), and also juvenile fish (28%) were most important. Among the other forage organisms, in 1962, *Callizona* sp. supplied 32.9%, and squid supplied 46.8% to 54.6%; in 1964, 59.7% in 1970, 75.7% in 1998 and in 2000, 43.3% of food weight. Sockeye had the widest spectrum of food in the 1950s and 2000s (18 and 26 components, respectively). In the 1950s, stomach fullness was the lowest ($18–31°/_{ooo}$), whereas in the 1970s it was the highest ($33–67°/_{ooo}$). Sockeye salmon, as the most active competitor, did not change its principal food item. Only in the 1960s was the percentage of euphausiids nearly equal to that of juvenile squid. We conclude that the most stable and active consumer of crustaceans is sockeye salmon. Pink salmon compete with sockeye salmon, The most flexible consumer of various organisms is chum salmon.

BASIS Program Studies

Scientists from TINRO-Centre in three research vessels (Russian, American and Japanese) collected samples from salmon and processed them using the standard method ac-

cepted at TINRO-Centre (Chuchukalo and Volkov 1986; Volkov 1996). This method includes mass processing of stomach-enteric tracts immediately after catching without preservation. This method allows scientists to estimate the digestion stage of food, and, more important, to process all materials collected immediately while still at sea. The immediacy allows researchers to gain insights about the features and intensity of salmon feeding in each area surveyed. The basic juvenile salmon diets in the autumn of 2002–2004 consisted of hyperiids, (21.3–98.4% of food weight) (Fig. 5). In 2002 the dominant component was euphausiids (40.5%), but the portion of copepods (19.9%) and of arrow worms (14%) was also significant. In 2003 the sockeye diet also included pteropods (18.3%). The food spectrum of juvenile sockeye salmon was narrow (2–7 components), and stomach fullness was low (99–160°/$_{ooo}$).

Juvenile pink and chum salmon had wider food spectra (6–10 and 4–10 components, respectively). In 2002 the food spectrum of juvenile pink salmon included a high percentage (36.9%) of euphausiids, and in 2003 a high percentage (24.5%) of pteropods. The same species of plankton in the same years contributed a relatively high percentage in juvenile chum diets, 16.6 and 19.3% respectively. The stomach fullness of juvenile pink and chum salmon was also high (174–232°/$_{ooo}$ and 110–288°/$_{ooo}$, respectively).

Maturing chum and sockeye salmon had wider spectra of food than pink salmon (11–17 and 11–13 components, respectively) (Fig. 6). The ratio between spectra varied significantly by year. In 2002 and 2004 the basic chum diet consisted of juvenile fish (40.9% and 37.6%, respectively), hyperiids (25% and 18.2%, respectively) and euphausiids (13.6% and 30%, respectively). In 2003, chum salmon fed on pteropods (32.9%), hyperiids (9.5%) and juvenile fish (8.1%); approximately 40% of the food consisted of an extensively digested component whose composition could not be identified.

The stomach fullness of chum salmon varied from 29 to 59°/$_{ooo}$. Variations in fullness in sockeye salmon were high, from 15 to 70°/$_{ooo}$. The basic sockeye diet in 2002 and 2004 consisted of hyperiids (34.1% and 42%, respectively), euphausiids (15.5% and 25.6%, respectively), larval crabs (16.3% and 13.7%, respectively) and juvenile fish (10.3% and 14.4%, respectively). In 2003 chum fed on juvenile squid (39.4%), hyperiids (21.2%), pteropods (10.7%) and euphausiids (9.3%).

Thus, in the western Bering Sea, the dominant items in the diets of pink, chum and sockeye salmon were hyperiids, pteropods and small squid. The percentage of euphausiids was comparatively small. This could be explained firstly by the abundance of this plankton and secondly by the availability of these animals during the day when salmon feed most actively (Volkov and Kosenok 2005; Koval 2005). Interannual dynamics of the role of pteropods in salmon diets relates first of all to the peculiarities of the biology of this taxon (Volkov 2003). The highly abundant copepods and
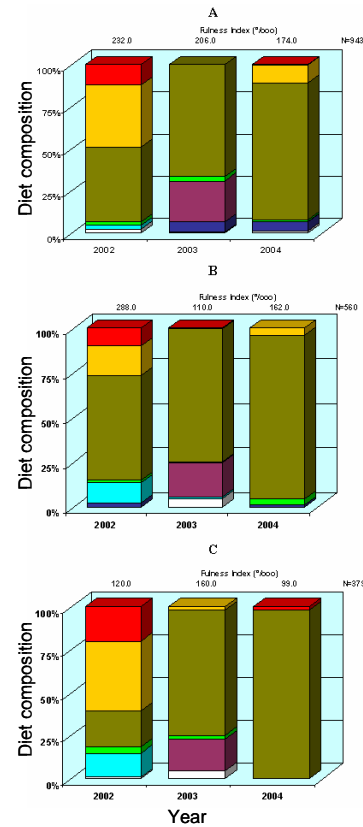
Fig. 5. Diet composition of juvenile pink (A), chum (B) and sockeye (C) salmon (2002–2004) from the BASIS program. Key as in Figure 1.
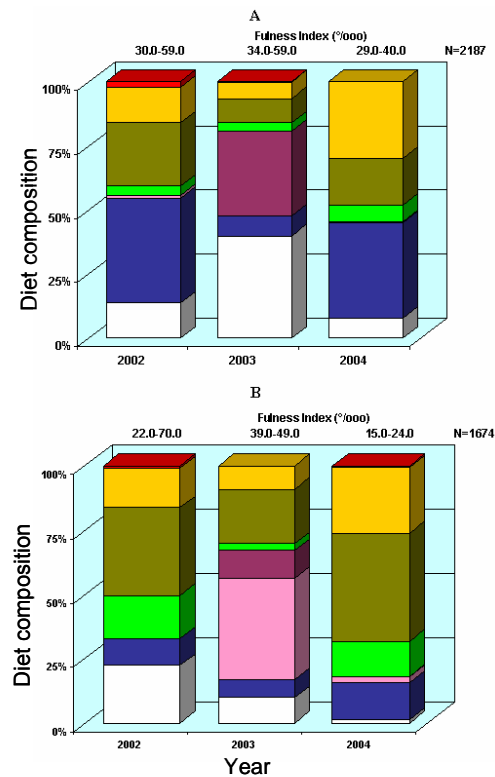
Fig. 6. Diet composition of immature chum (A) and sockeye (B) salmon (2002–2004) from the BASIS program. Key as in Figure 1.

Chaetognatha made up only a small percentage of salmon food weight.

Comparison of Plankton Community Structure and Diets

The data collected during the BASIS program allow us to compare diet composition and plankton biomass in the western Bering Sea (Figs. 7 and 8). Summary characteristics (distribution) of these parameters (plankton biomass and food composition) were similar, on the whole, as fractions–hyperiids, euphausiids, and so on. This is the foundation for our conclusion, that Pacific salmon are the best "plankton and nekton gear," and can be used for estimating the pro-
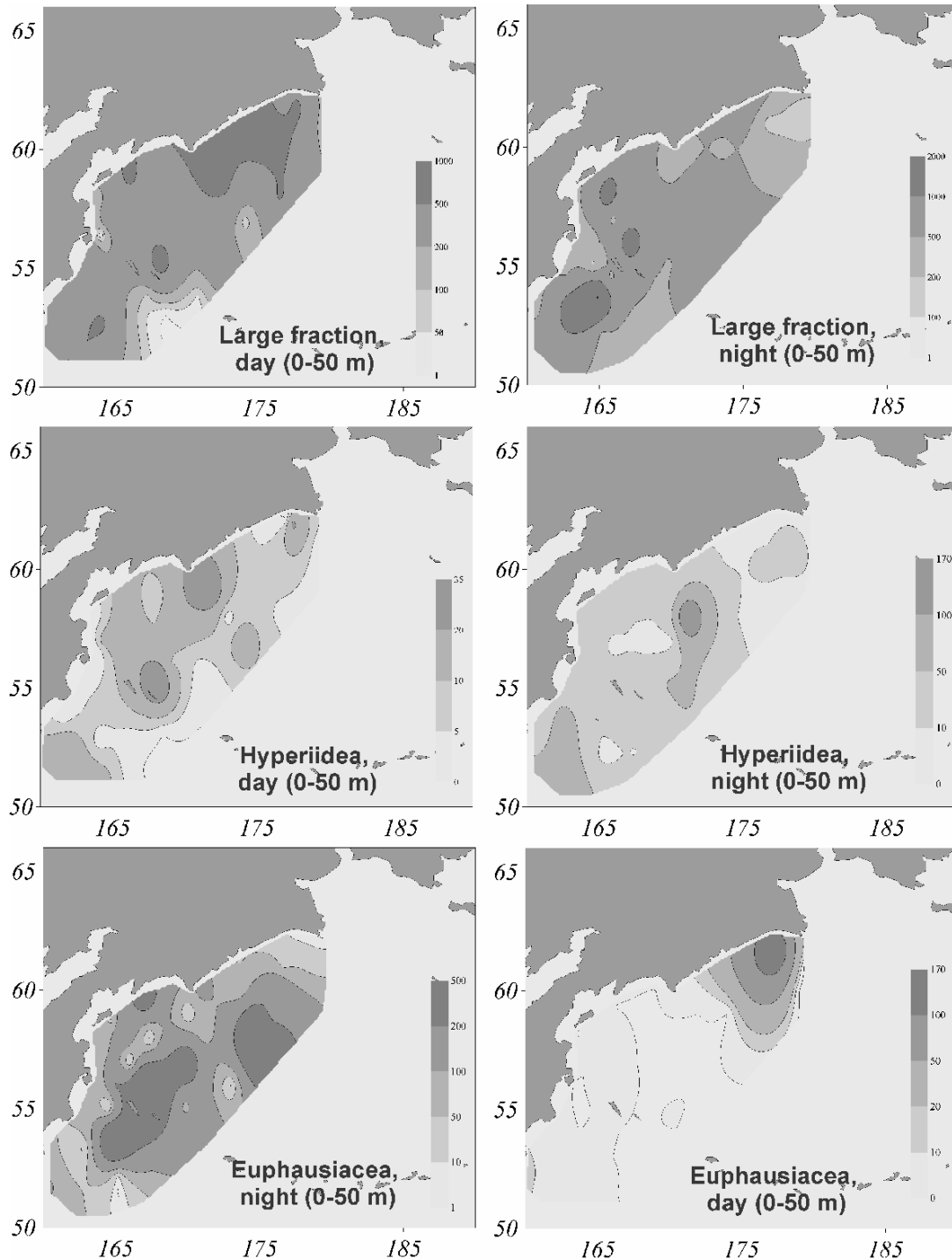
Fig. 7. Biomass (mg/m³) of zooplankton at 0–50 m during day and night in the western Bering Sea and North Pacific Ocean (Source: BASIS).

ductivity of these planktonic organisms, for seasonal, intra-annual, and interannual comparisons.

Salmon Feeding Interactions

The composition of salmon diets is determined by the abundance of forage organisms in the areas where salmon feed, and the dynamics of inter- and intra-specific feeding interactions. To provide an analysis of the character of salmon feeding interactions we have tried to analyze variations in the number of components and the structural composition of juvenile and adult salmon food in the areas of long-term
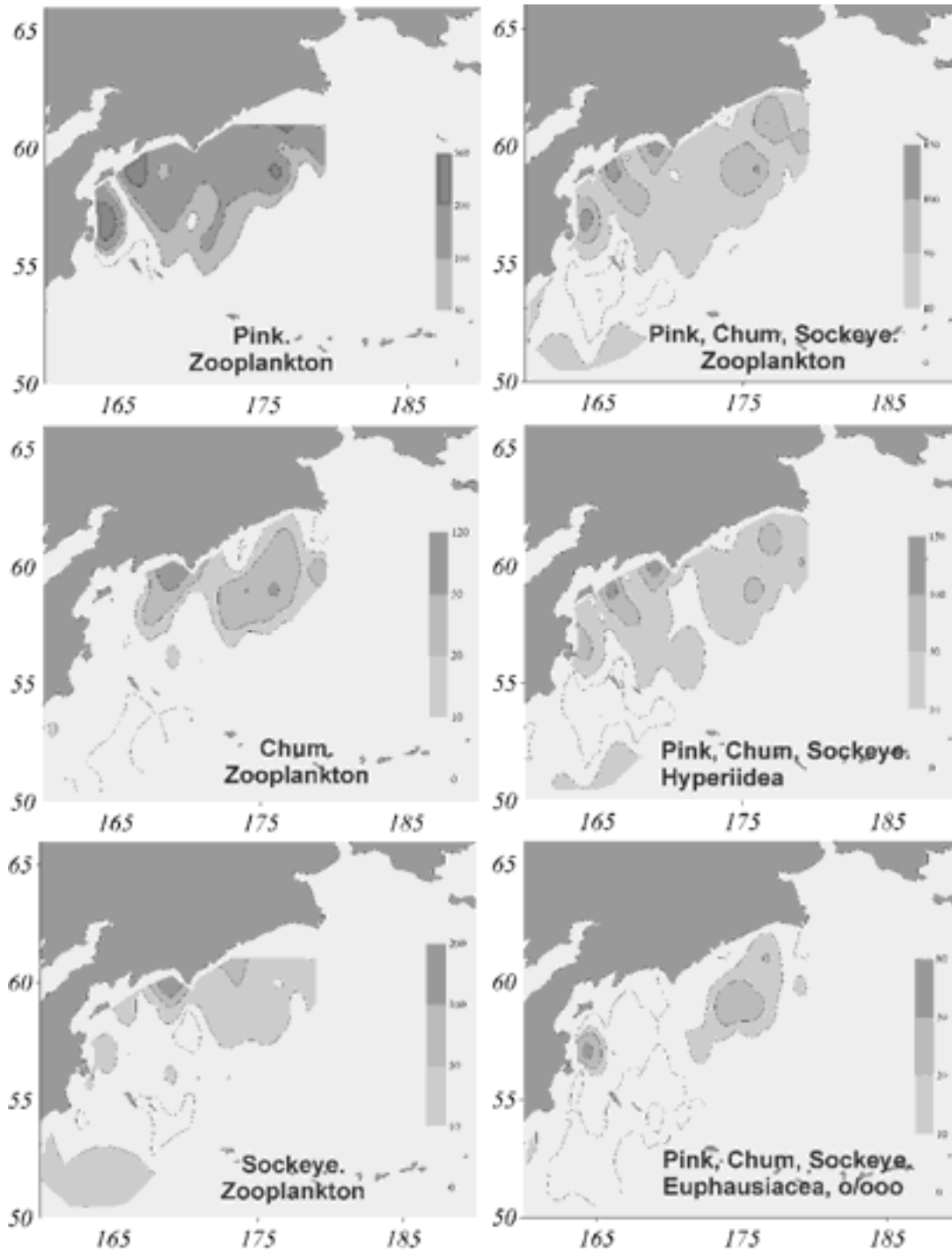
Fig. 8. Diet composition ($^0/_{000}$) of pink, chum and sockeye salmon (both individually and grouped together) in the western Bering Sea and North Pacific Ocean (Source: BASIS).

monitoring programs. We also tried to compare food similarity or food overlap (FS-coefficients).

Juvenile salmon

Diets of juvenile pink, chum and sockeye salmon have been recorded for nearly 40 years (1966–2002) in the Sea of Okhotsk (Fig. 9A). The diets of juvenile sockeye salmon had the smallest number of components (from 5 to 11), in comparison with the other species. In the late 1990s and early 2000s (in 1997, 1999 and 2001, specifically) the food spectrum for sockeye increased to up to 20 components. In recent years the widest food spectrum was seen in juvenile chum (up to 25 components) and pink salmon (up to 30 components). Also in recent years the highest abundance of feeding juvenile salmon, pink salmon in particular, was observed. The food spectrum for pink and chum usually included from 9 to 17 components and it did not vary significantly in either species by year.

In the Okhotsk Sea, diets of salmon juveniles of the three species used to show maximum food similarity, which can indicate favorable feeding conditions and a high level of the salmon forage base. For example, average FS-coefficients are usually over 50%, reaching up to 71% in pink and chum salmon; the lowest FS-coefficient (47.2%) was found in chum and sockeye (Fig. 10A). Moreover a higher food similarity was observed in the 1960s (90% to 100%) and 2000s (70% to 76%), and the minimal food similarity was seen in 1974 (33.4%) and 1983 (39%). The diets of pink and sockeye salmon had maximum food similarity in 1967 (75%), 1973 (83.9%) and 1986 (73.4%), and minimum food similarity in 1972 (9.5%). Minimum food similarity was also characteristic of chum and sockeye salmon (FS = 9.5% in 1972). These species had maximum food similarity in 1967 (89%) and 1981 (72.6%).
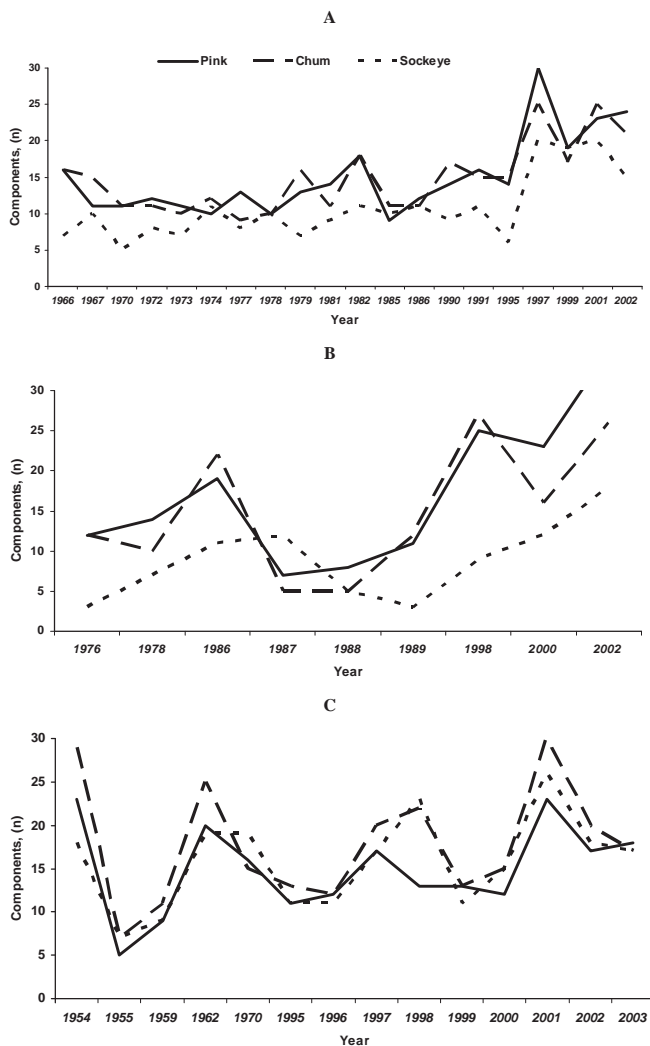

Fig. 9. Number of food components in the diets of pink, chum and sockeye salmon. A - juveniles, Okhotsk Sea, 1966–2002; B - juveniles, Bering Sea, 1976–2002; C - adults, North Pacific Ocean, 1954–2003.
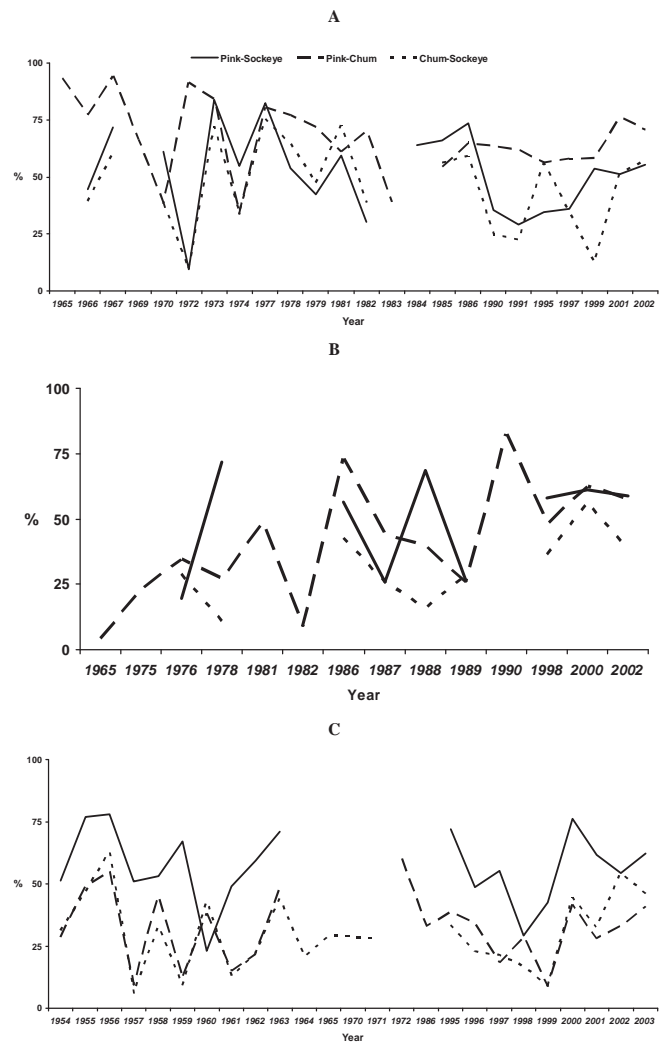

Fig. 10. FS-coefficients for pink, chum and sockeye salmon. A - juveniles, .Okhotsk Sea, 1965–2002; B - juveniles, Bering Sea, 1965–2002; C - adults, North Pacific Ocean, 1954–2003.

For the 9-year period of observation in the Bering Sea (BASIS), the narrowest food spectrum (3 to 18 components) was recorded for sockeye salmon (Fig. 9B). The food spectrum of the other two other species was twice as wide (5 to 35 components). Similar to those in the Sea of Okhotsk, the spectra of the two latter species increased substantially in the late 1990s to the early 2000s, coincident with a high abundance of juvenile pink and chum salmon. Comparative analysis of variations in food component number in pink salmon and chum salmon also has indicated this alternation.

Maximum FS-coefficients were observed between juvenile pink and sockeye salmon, averaging 50%. Minimum FS coefficients were seen in 1976: 19.9%; maximum values in 1978: 71.6% (Fig. 10B). The food similarity between pink and chum salmon; and also between chum and sockeye salmon was 5–10% less. In the first case it varied from 4.3% (1965) to 82.2% (1990) and in the second case from 11% (1978) to 56.6% (2000). Low FS-coefficients were observed when crustaceans were least important in the diets of juvenile chum salmon.

Adult salmon

In the Bering Sea the number of components in adult salmon diets (a 5-year observation period) was similar, except in 1996 when the number of components in the adult pink salmon diet decreased by half. In odd years the food spectrum was a bit wider in all species, which most likely was related to the high abundance of pink salmon. This occurred even though the diet compositions, as noted above, were very different.

Food similarity among adult salmon was lower when compared with juveniles, rarely exceeding 40%. Also the most similar diets were seen in pink and sockeye salmon – from 41.1% (1997) up to 75% (1983). Pink-chum FS-coefficients varied from 12.8% (2000) to 47.3% (1997). Chum-sockeye FS-coefficients ranged from 13.5% (2000) to 61.2% (1998).

The data record of diets of adults of the three species of salmon in the Pacific Ocean waters off Kamchatka extends from 1954 to 2003. The number of food components varied from 5 to 30, with the food spectrum of chum salmon usually being the widest (Fig. 9C). Recently, the widest food spectra have been seen in the three species of adult salmon. The number of food components was not significantly different among the three salmon species during the period of observation. An exception is 1998 when the pink salmon diet consisted of 13 components only, while chum and sockeye diets consisted, respectively, of 22 and 23 components. Maximum food diversity was seen in chum salmon; the minimum, in pink salmon. Sockeye salmon were intermediate between the two.

Diet comparisons among the three species showed maximum diet similarity between pink and sockeye salmon, and minimum diet similarity between chum and sockeye salmon. The highest FS-coefficients (77%–78%) were found for pink

and sockeye in 1955–1956, and the lowest (23% and 29.2%, respectively) in 1960 and 1998 (Fig. 10C). Pink-chum diet similarity ranged from 8.6% (1999) to 60% (1972). Chum-sockeye diet similarity ranged from 6% (1957) to 63% (1956). This is related to a high feeding liability of chum salmon in comparison with the other species. In general, diet similarity between pink and sockeye salmon is almost twice as high as that between pink and chum salmon or between chum and sockeye salmon.

Influence of Feeding on Biological Parameters of Fish

Salmon feeding conditions determine the timing of maturation, age composition of spawning fish and biological parameters such as length and weight. Moreover, the conditions often help explain the variations in the timing of salmon spawning runs. The variations range from several weeks early to later-than-normal timing, which, in turn can determine the effectiveness of the fishery for particular salm-
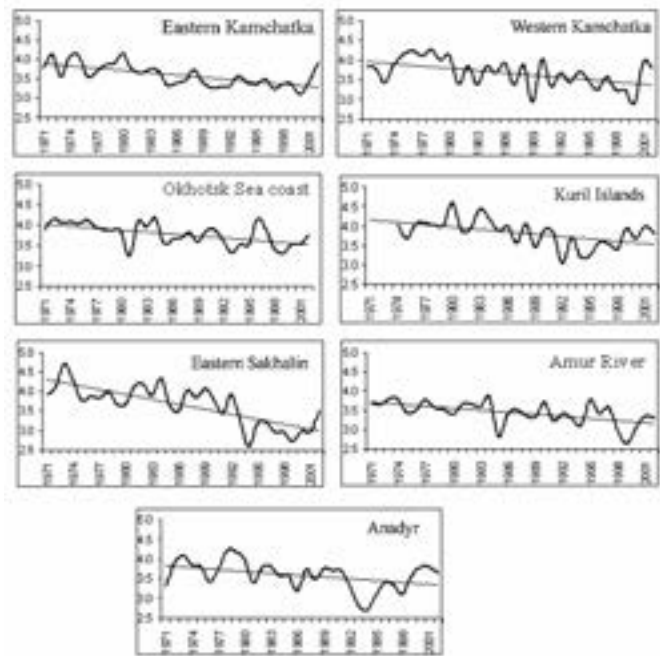

Fig. 11. Average weight (kg, on the y-axis) of chum salmon from commercial catches in different areas of the Russian Far Eastern Seas, 1971–2002.
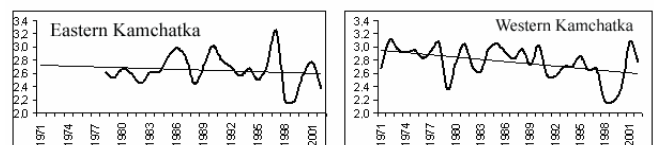

Fig. 12. Average weight (kg, on the y-axis) of sockeye salmon from commercial catches in eastern and western Kamchatka, 1971–2002.

on species.

In the course of our analysis of salmon length variations for the years following the period of serious depression in the 1960s–1970s, we noted that different species show different tendencies. For example, in most regions the average weight of pink salmon in spawning runs increased, with the exception of the southwestern Sakhalin pink salmon run. The reason, apparently, is that a principal part of this pink salmon stock feeds in the Sea of Japan, where forage resources are limited. For most other stocks that feed in the high seas areas of the Pacific Ocean, a significant increase in size is characteristic. For example this pattern is seen in the West Kamchatka, East Sakhalin and Kuril pink salmon stocks (Karpenko and Rassadnikov 2004). The average weight of sockeye salmon and of chum salmon, in particular, decreased during the same period (Figs. 11 and 12) (Karpenko and Rassadnikov 2004). Moreover, a maximum decrease was observed particularly in the regions where the maximum growth of pink salmon had been recorded. Since the late 1980s an increase in the percentage of older chum salmon in spawning runs has been recorded, especially for the northeastern Kamchatka populations (Gritsenko et al. 2000; Zavarina 2001, 2003, 2005), the northern coast of the Okhotsk Sea (Volobuev 2000;Volobuev and Volobuev 2000), and also for the North American chum salmon (Bigler et al. 1996; Helle and Hoffman 1995, 1998). In the twenty-first century the average weight of chum salmon has been increasing, which has been shown, in particular, for the fish from East Sakhalin, Kamchatka and Anadyr (Karpenko and Rassadnikov 2004).

Our data indicate, that the maximum influence on the development of biological parameters, including size and age composition of adult fish (sockeye and chum salmon in particular), has been shown by pink salmon, the most abundant salmon species in Asia. Sockeye salmon, as a food competitor, is the next most abundant, with chum salmon being the most vulnerable species. Studying the trophic interactions of pink, chum and sockeye salmon clearly allows us to obtain insights into the state of pelagic ecosystems in the North Pacific Ocean.

CONCLUSIONS

Our analysis of pink, chum and sockeye diets leads us to suggest the following:

1. The Pacific salmon is the best "plankton gear". The diets of pink, chum and sockeye salmon are a good indicator of the state of plankton and nekton communities in regions of the North Pacific Ocean, reflecting the development and composition of these communities. The level can be figured out by judging the composition of food and intensity of feeding of the adult fish, and also the migration routes of juvenile fish from the rivers to the sea.

2. Among the three salmon species studied, the best indicator of plankton production and community composition is the chum salmon because it is the most flexible consum-

er of marine plankton in forage zones of the North Pacific Ocean. In poor forage conditions, chum salmon consume a high percentage of organisms of low caloric value. Such diets are thought to result in lowered growth rates and rates of maturation of returning adults.

3. More accurate assessment of the forage resources in regions of the North Pacific requires intense study of the long-term variations in the pelagic community - the interactions not only between particular salmon species, but between salmon and the structure of plankton, and dynamics of the abundance of other plankton consumers and the volume of food they are consuming.

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Regional Diversity of Juvenile Pink Salmon Diet in Autumn in the Bering, Okhotsk and Japan Seas

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Abstract: Regional variability in the diet of juvenile pink salmon was studied in the Bering, Okhotsk and Japan seas during the autumn of 2002–2004. During this time young pink salmon preyed mainly upon ichthyo- and mero-plankton in the eastern Bering Sea. In the Okhotsk, western Bering and northwestern Japan seas the most frequently occurring prey items in the juvenile pink salmon diet were planktonic crustaceans: hyperiids (*Themisto pacifica*, *T. libellula* and *Primno macropa*), euphausiids (*Thysanoessa longipes*), copepods (*Neocalanus plumchrus*) and pteropods (*Limacina helicina*). Other food organisms (irrespective of their high biomass in the pelagic plankton community) were of secondary importance or would only occur occasionally in fish stomachs. We suspect that food habits of juvenile pink salmon were associated with the accessibility of forage groups in the habitat strata of juvenile pink salmon. In the upper epipelagic layer (0–50 m), the biomass of zooplankton (particularly copepods and euphausiids) increased at night due to vertical migrations from deeper layers, while hyperiids and pteropods (small- and medium-size *L. helicina*) were present in dense aggregations in the surface layer during day and night hours. However, juvenile pink salmon consumed prey mainly during daylight hours. Thus, juvenile pink salmon preyed upon plankton groups and species that were more abundant in habitat strata of juvenile pink salmon during daylight hours.

Keywords: juvenile pink salmon, diet, stomach contents, prey composition, Japan Sea, Okhotsk Sea, Bering Sea

INTRODUCTION

Juvenile Pacific salmon are among the main consumers of forage resources in the upper epipelagic layers in the Bering, Okhotsk and Japan seas during autumn. This raises an interest in the study of food habits, forage demands and trophic relationships of juvenile Pacific salmon. An extensive database on the ecology and forage activity of Pacific salmon species has been collected during the last decades in TINRO-Centre expeditions into the Far Eastern seas. Simultaneous studies were conducted in the Okhotsk, Bering and northwestern Japan seas in autumn 2002–2004. Data collected in these studies made it possible to compare food habits of pink salmon from different regions of the Far Eastern seas under various forage base conditions.

MATERIALS AND METHODS

In this study, we present data on food habits of juvenile pink salmon and on the composition of plankton, collected in autumn 2002–2004 in the Japan, Okhotsk and Bering seas. Field data were collected on TINRO-Centre research vessels and also on the R/V *TINRO*, R/V *Sea Storm* and the R/V *Kaiyo maru*, under the international research program Bering-Aleutian Salmon International Survey (BASIS). A total of 411 plankton stations were sampled in the epipelagic zone (0–50 m), and a total of 5,125 juvenile pink salmon stomachs were examined (Table 1).

The trawling surveys of the upper epipelagic layer in the northwestern Japan, Okhotsk and western Bering seas were conducted using a standard midwater rope trawl (the length of the headrope is 80 m, and the perimeter of the trawl opening is 396 m). The trawl hydrodynamic plate (6 m², 0.6 x 10 m) had floats on the headrope. The trawl was 30 m long with quadrangular mesh in the body and wings and a small mesh codend.

Standard methods, developed earlier and widely used in TINRO-Centre studies (Volkov and Chuchukalo 1986), were used for collecting data and the analyses of fish stomach contents. We combined stomach contents from fish of one size (for pink, 10–20 and 20–30 cm) from each trawl sample, and identified prey items, total prey weight and weight of each prey component. After that we calculated mean values for the sample and for each region.

Plankton stations were sampled with a Juday Net (nylon, with a 0.168-mm mesh; mouth opening area 0.1 m²) in the epipelagic layer (0–50 m and 0–200 m) during both day and night before trawling for nekton. Samples of plankton were

subdivided into three size groups: small (animals < 1.2 mm in length), medium (animals 1.2–3.2 mm) and large (animals > 3.2 mm). After that, we analyzed species composition of a sample, and weight, size and developmental stages for each species. The biomass was determined using a volumeter. We also incorporated net catchability coefficients (CC) in calculations of abundance and biomass for each plankton

Table 1. The numbers of stations and stomachs analyzed, by area.

	Number of stations	Number of stomachs analyzed
Western Bering Sea	131	1,427
Eastern Bering Sea	114	692
Sea of Okhotsk	114	2,252
Northwestern Japan Sea	52	754
Total	411	5,125

Table 2. Catchability coefficients for different plankton size groups (from Volkov 1996a).

Plankton size groups	Catchability coefficients (CC)
Small (animals < 1.2 mm)	1.5
Medium (animals 1.2–3.2 mm)	2.0
Large (animals > 3.2 mm):	
euphausiids < 10 mm	2.0
euphausiids 10–20 mm	5.0
euphausiids < 20 mm	10.0
chaetognaths < 10 mm	2.0
chaetognaths 10–20 mm	5.0
chaetognaths 10–20 mm	10.0
hyperiids < 5 mm	1.5
hyperiids 5–10 mm	5.0
copepods < 5 mm	2.0
copepods > 5 mm	3.0

Fig. 1. Biostatistical regions of data averaging: in the Okhotsk Sea (upper left): I–VI = northern regions, VII–VIII = Western Kamchatka, IX = central Basin, X = eastern shelf of Sakhalin, XI = Terpenya Bay, XII = southern Basin, XIII a = northern and b = southern Kuril regions, 7–10 = Pacific regions; in the northwestern Japan Sea (upper right): 1 = Tartar Strait, 2 = northern Primorye, 3 = southern Primorye, 4 = deepwater area; in the Bering Sea (lower panel): 1 = Bering Strait, 2 = northwestern Anadyr Bay, 3 = southeastern Anadyr Bay, 4 = eastern Anadyr Bay, 5 = Navarin region, 6 = Koryak shelf, 7 = Koryak slope, 8 = western Aleutian Basin, 9 = Olutorskyi slope, 10 = shelf of Karaginskyi and Olutorskyi bays, 11 = Karaginskyi slope, 12 = Commander Basin, 5p = Kamchatka Trench, 6p = oceanic waters off Kamchatka and Commander Islands, An = Anadyr Bay, WB = western Bering Sea basins, WP = oceanic waters near Commander Islands, CB = central deep Bering Sea, Nun = Nunivak region, Br(sw) = shallow area of Bristol Bay (< 50 m), Br(sh) = shelf zone of Bristol Bay (> 50 m) (from Shuntov et al. 1986; Shuntov et al. 1988a, b; Volkov et al. 2004).

species (Table 2).

All numerical data were averaged by standard biostatistical regions, which had been established based on water circulation schemes and distribution patterns of water masses (Fig. 1) (Shuntov et al. 1986; Shuntov et al. 1988a, b). Areas of data averaging based on BASIS expeditions in the eastern Bering Sea followed Volkov et al. (2004).

RESULTS

Juvenile pink salmon prey on a variety of planktonic and nektonic organisms (Volkov 1996b; Gorbatenko 1996a; Dulepova 1998; Lazhentsev and Bokhan 2001; Efimkin 2003; Efimkin et al. 2004; Volkov et al. 2006). Amphipods (hyperiids) and euphausiids were the predominant zooplankton prey during the entire research period. Pteropod mollusks may also be of high value as prey items. Copepods and chaetognaths were much less important. The amount of nektonic prey, such as larvae and juvenile fish (walleye pollock, capelin, sand lances and other species) and juvenile squid and crab, varied significantly (depending on the season and region). Prey composition in the diet of pink salmon depended on the seasonal abundance and vertical distribution of prey organisms in a particular area. The composition of species and groups of plankton, which formed the forage base for juvenile pink salmon, varied among the Bering, Okhotsk and Japan seas.

Bering Sea

Research conducted in 2002–2004 revealed that the composition of the forage base for Pacific salmon was different in the western, central and eastern parts of the Bering Sea. Large-sized zooplankton dominated plankton communities in the upper epipelagic layer in the western and central Bering Sea. Small- and medium-sized zooplankton were more abundant in the upper epipelagic layer in the eastern Bering Sea (Fig. 2). The dominant groups in the eastern Bering Sea plankton communities in autumn were ichthyoplankton and meroplankton (Efimkin et al. 2004; Volkov et al. 2004, 2006).

The study of Pacific salmon food habits reveal that in September–October of 2003–2004, in the eastern Bering Sea (shallow and shelf zones of Bristol Bay and Nunivak region) juvenile pink salmon preyed mainly upon larvae and juveniles of walleye pollock and capelin, crab larvae and larvae of bottom fish (Fig. 3) (Efimkin et al. 2004; Volkov et al. 2006).

In upper epipelagic layers of the western Bering Sea during autumn 2002–2004, copepods (mainly *Neocalanus plumchrus*, *Calanus glacialis*, *Metridia pacifica*, *Eucalanus bungii*, and *Oithona similis*) and chaetognaths were the predominant groups in the zooplankton community. Maximum copepod biomass ranged from 163.9–1280.3 mg/m³ in coastal areas and 75.5–498.8 mg/m³ in the deep-sea areas; the bio-
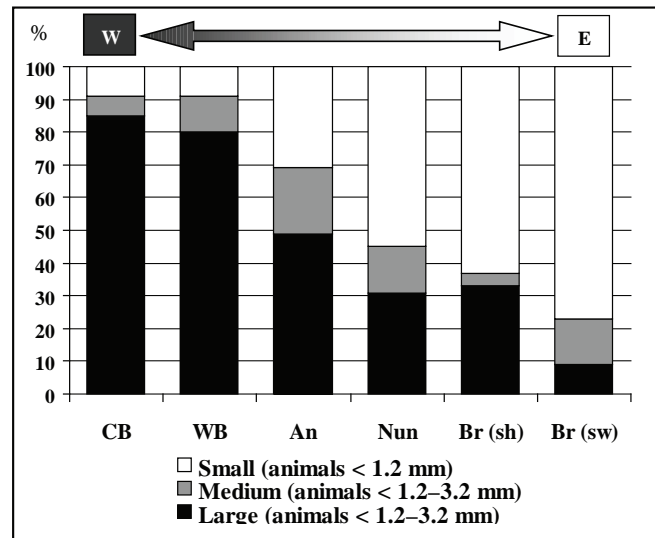
Fig. 2. Structure of plankton communities (%) in the epipelagic layer in the Bering Sea in autumn 2003–2004 (from Volkov et al. 2006 with modifications). Names of biostatistical regions according to Fig. 1.
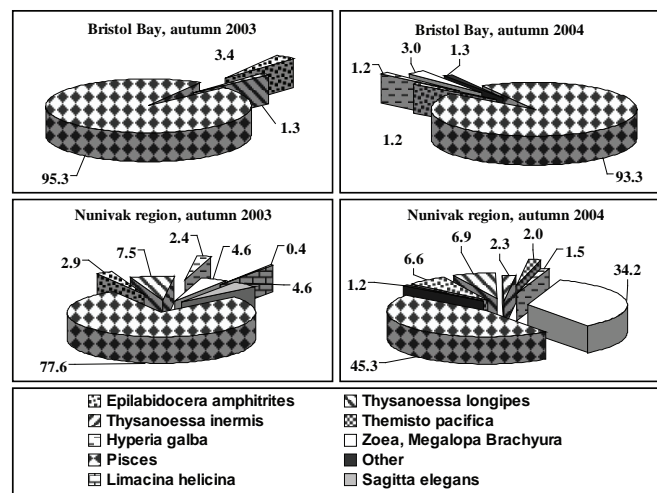
Fig. 3. Diet (%) of juvenile pink salmon in the upper epipelagic layer in the eastern Bering Sea in autumn 2003–2004 (from Efimkin et al. 2004; Volkov et al. 2006 with modifications).

mass of chaetognaths reached 101.9–420.2 mg/m³ in coastal areas and 124.1–288.7 mg/m³ in deep-sea areas. Pteropods and amphipods (mainly hyperiids) were more common in the Anadyr Bay and Navarin regions than in other areas (Fig. 4). Although copepods and chaetognaths dominated the zooplankton community, hyperiids, euphausiids and pteropods were the three most important food items in the juvenile pink salmon diet. For example, hyperiids (*Themisto pacifica* and *T. libellula*) and euphausiids (*Thysanoessa longipes*), whose abundance was relatively low, dominated in the juvenile pink salmon diet in the autumn of 2002 (Fig. 5). In the autumn of 2003, juvenile pink salmon preyed largely on pteropods (*Limacina helicina*), which accounted for up
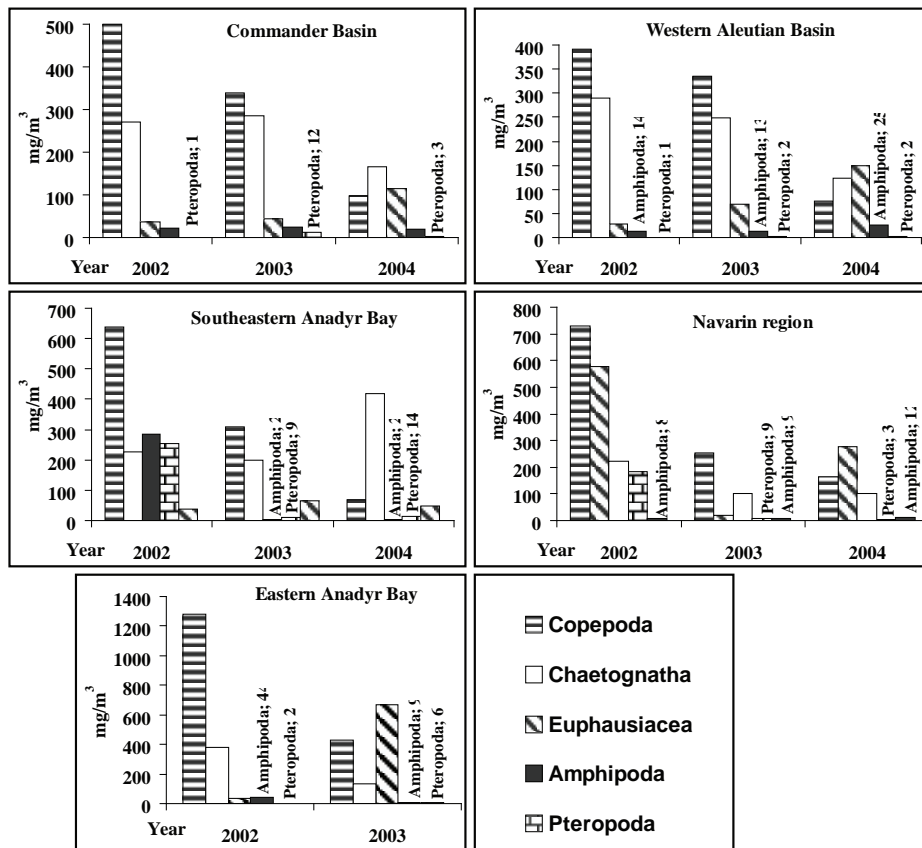
Fig. 4. Biomass (mg/m³) of some groups of zooplankton in the epipelagic layer in the western Bering Sea in autumn 2002–2004.
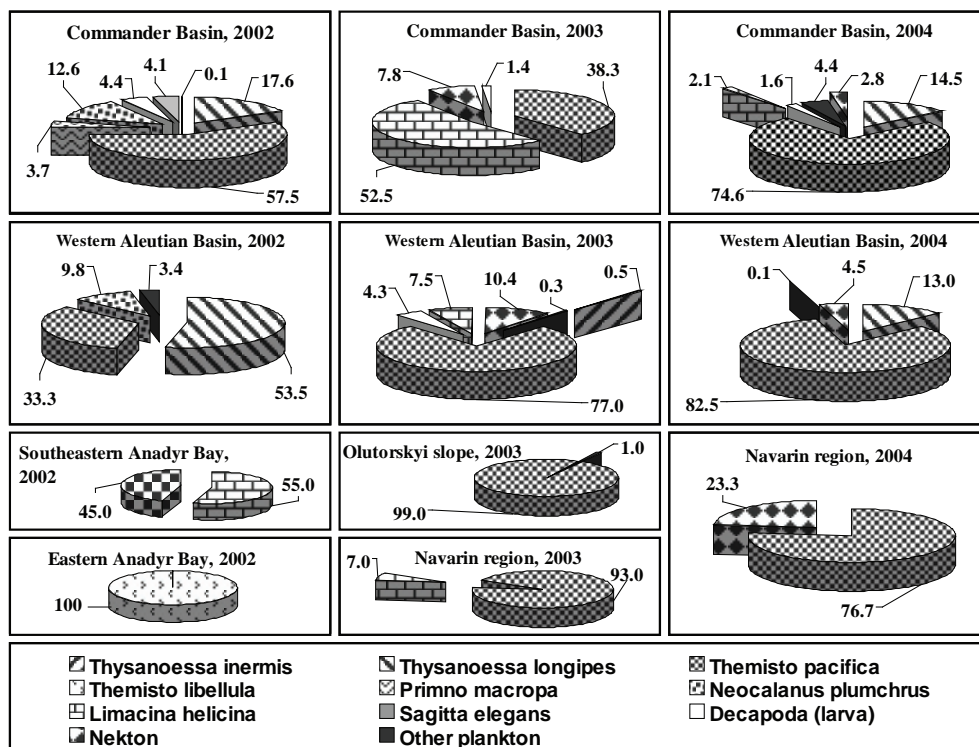
Fig. 5. Diet (%) of juvenile pink salmon in the upper epipelagic layer in the western Bering Sea in autumn 2002–2004.

to 53% of the fish diet in the Commander Basin. In this particular area, pteropods were more numerous than in the other regions of the sea, and accounted for 2% of the total zooplankton biomass. Biomass of pteropods in the Aleutian Basin was lower than in the Commander Basin; however, hyperiids were found in similar quantities in both areas (Fig. 4), and comprised major portions of the juvenile pink salmon diet in the Aleutian Basin (Fig. 5). In the autumn of 2004, the biomass of euphausiids was high and comprised from 8% to 49% of the zooplankton biomass depending on the area (Fig. 4). However, at that time they accounted for about 15% of the juvenile pink salmon diet, which was even less than in 2002. The hyperiid (*T. pacifica*) was the major prey of juvenile pink salmon in all of the research regions of the western Bering Sea in the autumn of 2004 (Fig. 5).

Okhotsk Sea

Euphausiids (mainly *T. longipes*, *T. inermis*, *T. raschii* and to a lesser extent *Euphausia pacifica*), copepods (mainly *N. plumchrus*, *M. pacifica*, *M. okhotensis*, *Pseudocalanus minutus*, and *O. similis*) and chaetognaths dominated the zooplankton community in most areas of the Okhotsk Sea.

The maximum biomass of euphausiids (195.3–1077.0 mg/m³) was located in the southern Okhotsk Sea, particularly in the coastal waters of eastern Sakhalin and Terpenya Bay. A high biomass of hyperiids (118.7–193.0 mg/m³) was also found in these areas. The biomass of copepods and chaetognaths varied among the Okhotsk Sea areas, and their total biomass in the Okhotsk Sea was notably lower than in the Bering Sea (Fig. 6).

The diet of juvenile pink salmon was more diverse in the Okhotsk Sea than in the Bering Sea. Two hyperiids (*T. pacifica* and *Primno macropa*) and two euphausiids (*T. longipes* and *E. pacifica*) were the main prey items for juvenile pink salmon in the Okhotsk Sea in the autumn of 2002 (Fig. 7). However, juvenile pink salmon also consumed calanoid copepods, pteropods, and chaetognaths in notable quantities. A similar pattern of juvenile pink salmon food habits was observed in the autumn of 2003 (Fig. 7). It is worth noting that *P. macropa* comprised a large portion of the fish diet in 2002 and 2003 in spite of the fact that the biomass and occurrence of these hyperiids were low in the plankton community. The same was true for the pteropod mollusk *L. helicina*. The biomass of copepods (particularly *M. okhotensis* and *O. similis*) was high in the study area in 2004; however, juvenile pink
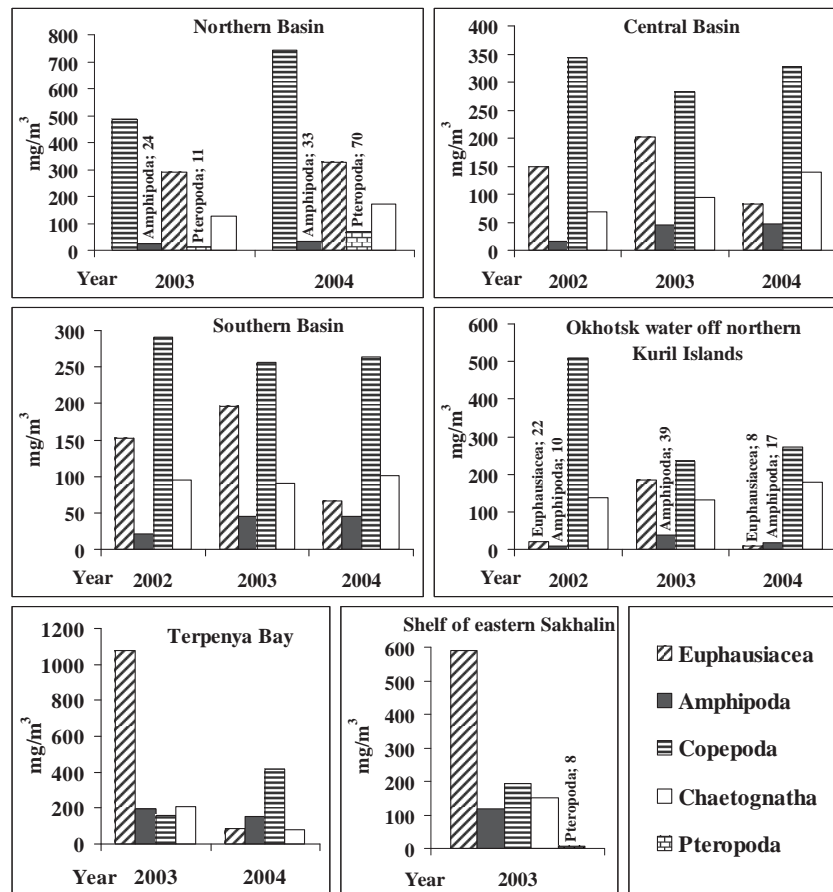
Fig. 6. Biomass (mg/m³) of some zooplankton groups in the epipelagic layer in the Okhotsk Sea in autumn, 2002–2004.
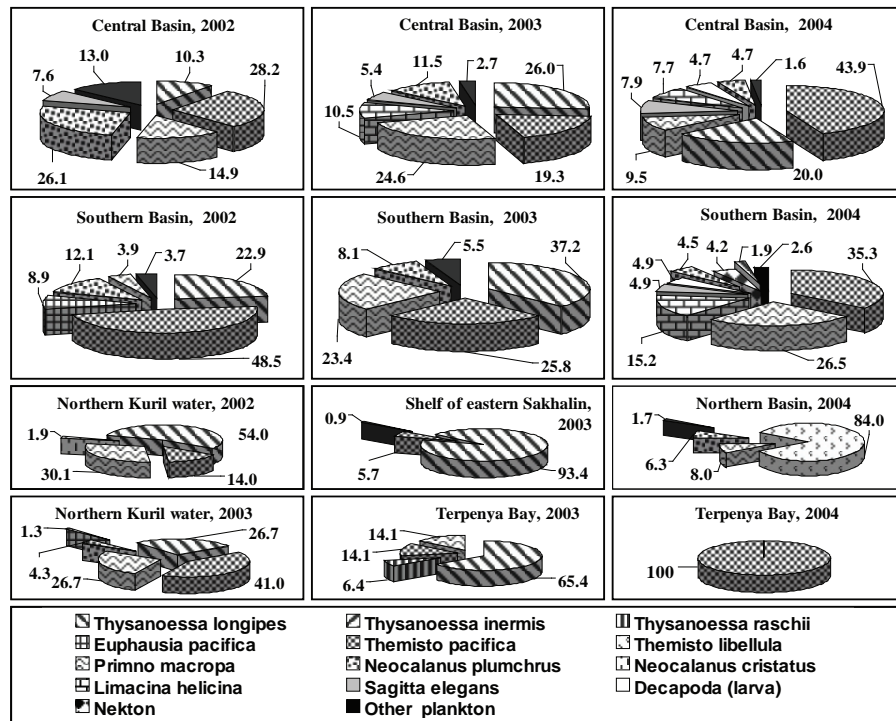
Fig. 7. Diet (%) of juvenile pink salmon in the upper epipelagic layer in the Okhotsk Sea in autumn 2002–2004.
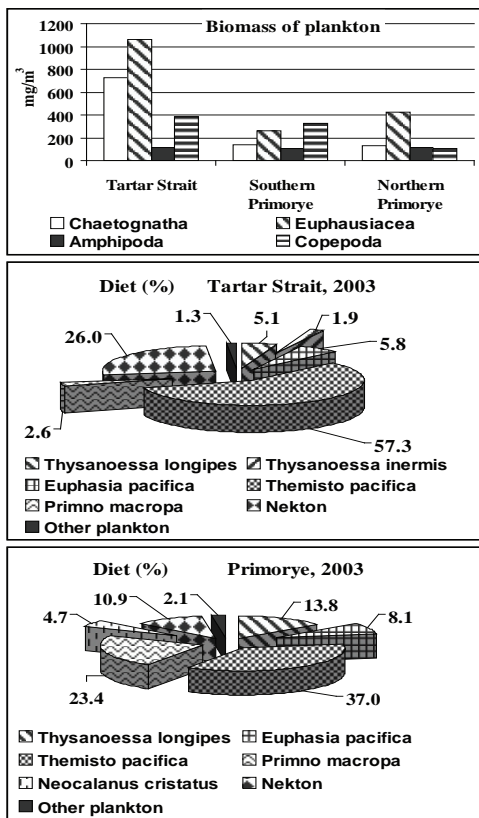
Fig. 8. The composition (mg/m³) of plankton community and diet (%) of juvenile pink salmon in the epipelagic layer in the northwestern Japan Sea in autumn 2003.

salmon did not consume these animals.

In the autumn of 2003, juvenile pink salmon preyed upon the highly abundant euphausiids and copepods in the northern Okhotsk Sea (Fig. 6). In the autumn of 2004, juvenile pink salmon preyed mainly upon the hyperiid *T. libellula* (Fig. 7).

Northwestern Japan Sea

Copepods (mainly *Calanus glacialis*, *M. pacifica*, *M. okhotensis*, *N. cristatus*, and *N. plumchrus*), chaetognaths, and euphausiids (*T. longipes*, *T. inermis*, and *E. pacifica*) comprised the bulk of the plankton community in the northwestern Japan Sea in the autumn of 2003 (Fig. 8). Hyperiids (*T. pacifica*) were more abundant, and pteropods (*L. helicina*) were less abundant in the plankton community in this area than in the Bering and Okhotsk seas. However, the share of *T. pacifica* in the juvenile pink salmon diet was lower in the Japan Sea than in the Bering Sea, because juvenile pink also preyed upon another hyperiid species (*P. macropa*) as well as upon euphausiids and juvenile fish, which were highly abundant in the upper epipelagic layer in the northwestern Japan Sea (Fig. 8).

DISCUSSION

In all regions except for the eastern Bering Sea, the most common prey items in the juvenile pink salmon diet were planktonic crustaceans: hyperiids (*T. pacifica*, *T. libellula*
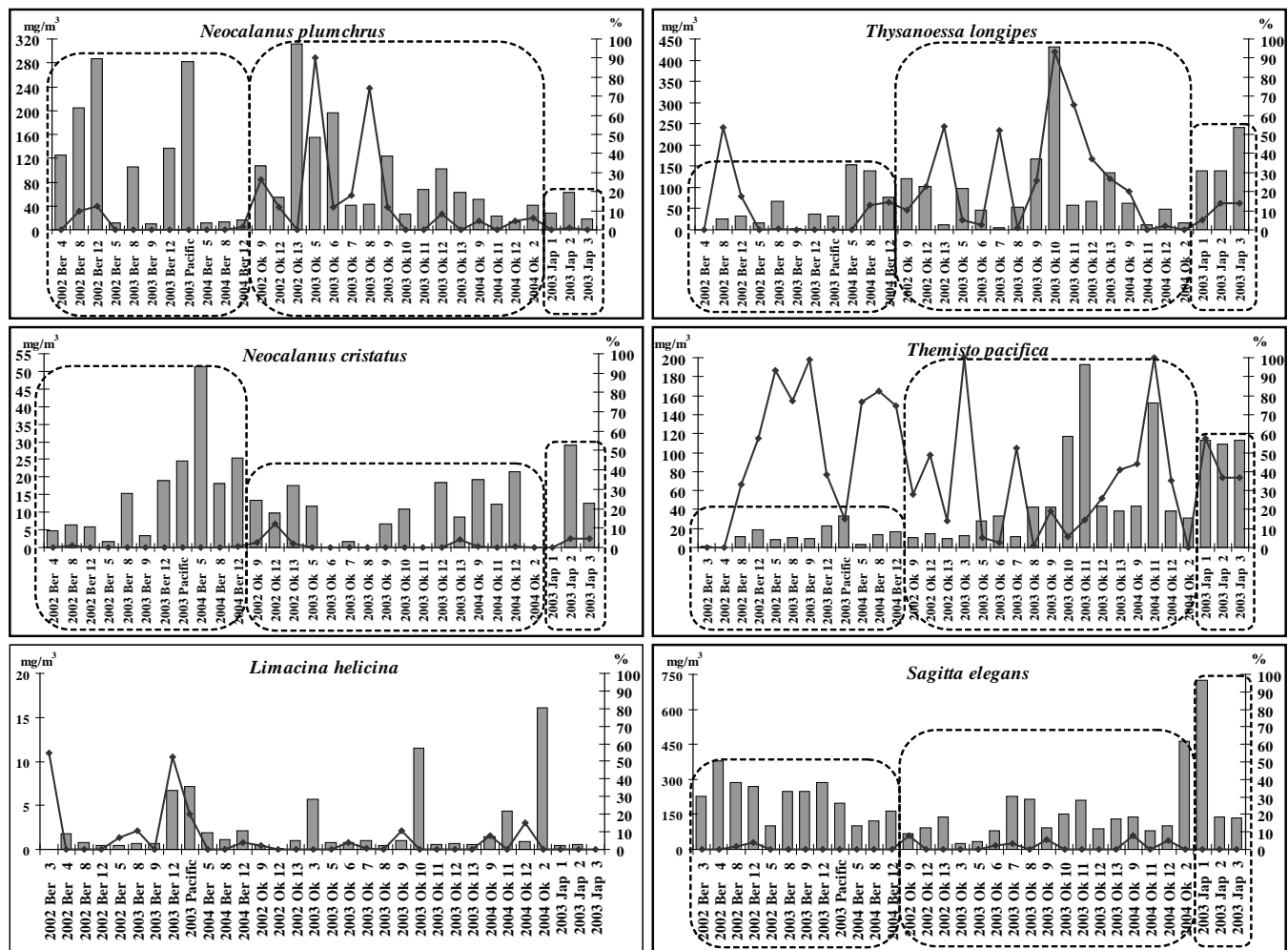
Fig 9. Biomass (mg/m³) of some species of zooplankton and their share in the juvenile pink salmon diet (%) in different areas of Far East seas in autumn 2002–2004. 2002, 2003, 2004 = years; Ber = Bering Sea, Ok = Okhotsk Sea, Jap = Japan Sea, Pacific = Pacific regions; 1–13 = number of biostatistical regions according to Fig. 1.

and *P. macropa*), euphausiids (*T. longipes*), copepods (*N. plumchrus*) and gelatinous mollusks (pteropods *L. helicina*). In some research regions the higher the biomass of euphausiids (*T. longipes*), copepods (*N. plumchrus*) and pteropods (*L. helicina*) in the pelagic plankton community, the higher was their proportion in the juvenile pink salmon diet.

However, hyperiids (*T. pacifica*) frequently occurred in the juvenile pink salmon stomachs irrespective of their biomass in the pelagic plankton community (Fig. 9). Copepods (*N. cristatus*, *M. pacifica*, *O. similis*, and *P. minutus*) and chaetognaths (*Sagitta elegans*) rarely occurred in juvenile pink salmon stomachs irrespective of their high biomass in the plankton.

We suspect that the food habits of juvenile pink salmon are associated with the accessibility of their forage groups in their habitat strata. Accessibility of zooplankton prey for juvenile pink salmon may be governed by different factors, in particular, by zooplankton vertical distribution patterns and diel migrations. Vertical sections of plankton distribu-

tion in the Bering Sea in September of 2003 and August of 2004, suggested that in the upper epipelagic layer (0–50 m), the biomass of zooplankton (particularly copepods and euphausiids) increased at night due to vertical migrations from deeper layers (Fig. 10). Similar results of vertical plankton distribution in the Far Eastern seas (including the Okhotsk and Japan seas) were obtained earlier (Vinogradov 1954; Gorbatenko 1996b). Euphausiids mainly aggregated at depths of 200–500 m during the day and migrated to depths of 150–200 m at night. But in those areas where biomass of euphausiids was very high (especially in the southern Okhotsk Sea), they occurred in the upper epipelagic zone (0–50 m) during the day and could serve as prey for juvenile pink salmon. Hyperiids (mainly *T. pacifica*) were present in dense aggregations during both day and night in the subsurface layer (0–10 m). The most dense aggregations of pteropods *L. helicina* (particularly small- and medium-size groups) were also distributed in the upper epipelagic layer, 0–50 m (Chuchukalo and Napazakov 1998; Volkov 2003).
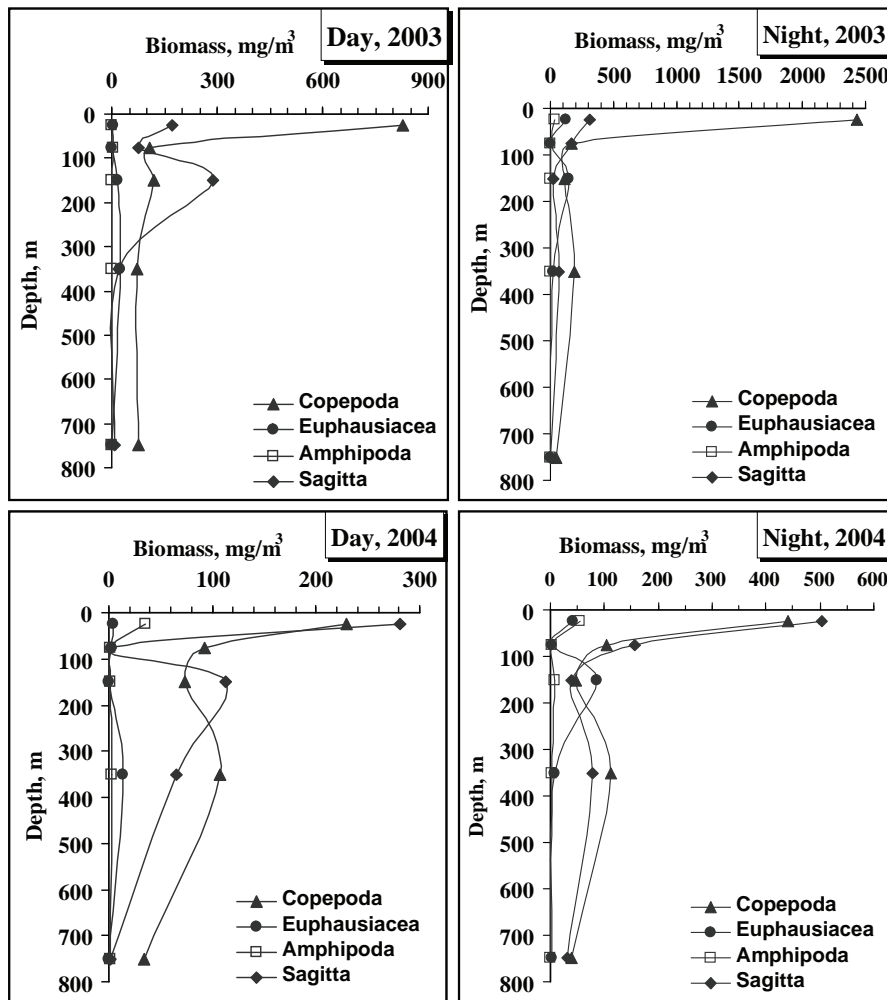
Fig. 10. Vertical sections of zooplankton at a daily station in the western Bering Sea from 8 to 9 September 2003 and from 23 to 24 August 2004 (A. Slabinsky, TINRO-Centre, Vladivostok, Russia, personal communication).
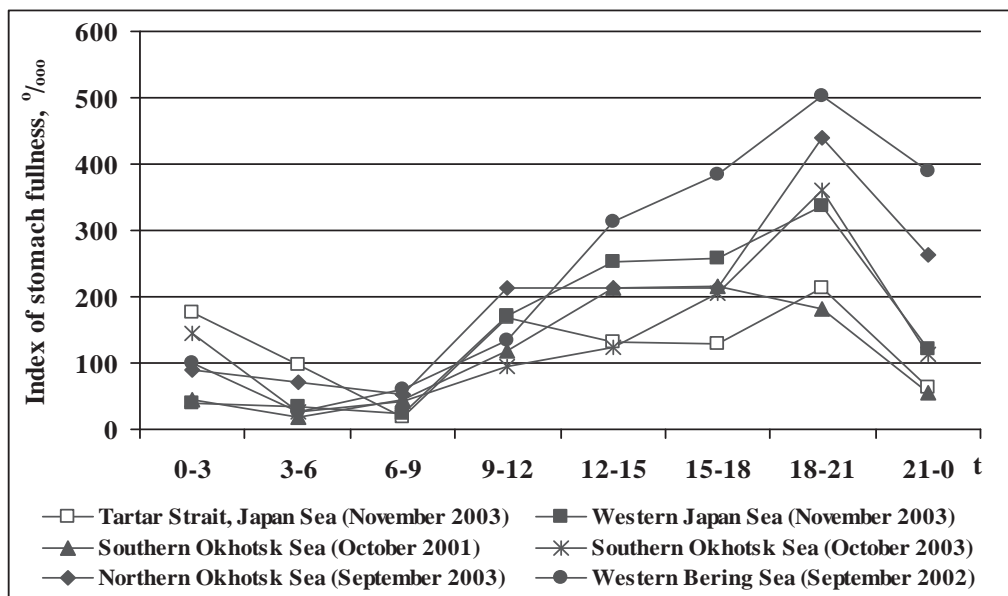
Fig. 11. Daily rhythm of juvenile pink salmon feeding in the Far Eastern seas in autumn.
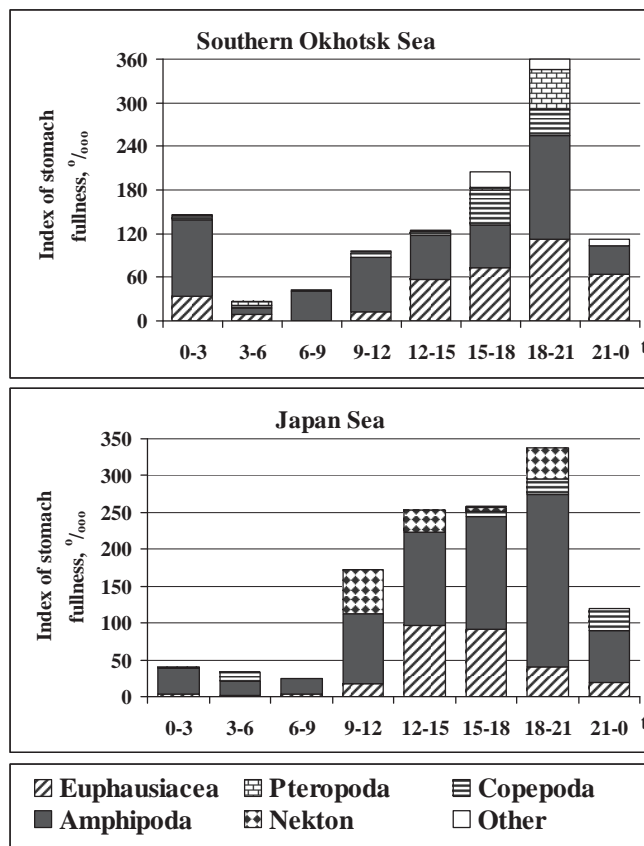
Fig. 12. Consumption of some zooplankton groups by juvenile pink salmon during day and night in the southern Okhotsk and northwestern Japan seas in autumn 2003.

High copepod abundance in the epipelagic zone was also observed at night, because most copepods tend to migrate to deeper waters during daylight hours. In August of 2004 in the western Bering Sea, the biomass of copepods averaged 440.4 mg/m³ at night and 229.9 mg/m³ during the day. Copepods (*N. plumchrus*: C IV and V stages of development) dominated among copepods during the day (138 mg/m³) and at night (165 mg/m³). Deep-water copepods (*N. cristatus*) did not occur in the upper epipelagic zone during the day, while at night their biomass increased up to 141.8 mg/m³. Copepods (*M. pacifica*: C IV and V stages of development and adult specimens) aggregated during the day at depths of 0–500 m, and at night part of the population concentrates at depths 10–50 m (Shebanova 1996). In September of 2003 in the western Bering Sea, the biomass of copepods (*M. pacifica*) increased up to 128.5 mg/m³ at 0–50 m; in 2004 copepods (*M. pacifica*) did not occur in the upper epipelagic zone during the day, and increased up to 23.2 mg/m³ in the upper epipelagic layer at night. Surface copepods (*O. similis*) occurred in the upper epipelagic layer during the day (70.4 mg/m³) and at night (62.8 mg/m³), while the biomass of the copepod genus *Pseudocalanus* increased in the upper epipelagic layer at night in 2004. The biomass of chaetognaths in the upper epipelagic layer also increased considerably at

night. In summary, species of zooplankton (and stages of development) vary considerably in their vertical distribution and diel vertical migrations. Accordingly, the consumption of different species of zooplankton by juvenile pink salmon (or their share in the diet) changed during the day.

It is a well-known fact that juvenile pink salmon consume prey mainly during the day, between 10:00 a.m. and 10:00 p.m. (Gorbatenko 1996a; Lazhentsev and Bokhan 2001; Efimkin 2003). During autumn (for example, in the western Bering Sea in September, 2002, in the northern and southern Okhotsk Sea in September–October 2001 and 2003, and in the northwestern Japan Sea in November, 2003) the weakest forage activity of juvenile pink salmon was observed at night, while forage activity peaked between 3:00 p.m. and 9:00–10:00 p.m. (Fig. 11).

Juvenile pink salmon preyed primarily on zooplankton groups and species that were more abundant in the juvenile pink salmon habitat strata during daylight hours (Fig. 12). As a result, hyperiids (*T. pacifica*, *T. libellula* and *P. macropa*), euphausiids (*T. longipes*), copepods (*N. plumchrus*) and in some areas pteropods (*L. helicina*) were primary food items for juvenile pink salmon. Larvae, juvenile fish, and decapod larvae were primary food items for juvenile pink salmon in the upper epipelagic zone in the eastern Bering Sea, where these forage groups dominated the plankton community.

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Food Supply and Trophic Relationships of Pacific Salmon (*Oncorhynchus* spp.) and Atka Mackerel (*Pleurogrammus monopterygius*) in the Western Bering Sea in Fall 2002–2004

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Abstract: We examined the food supply and trophic relationships of pink (*Oncorhynchus gorbuscha*), chum (*O. keta*) and sockeye (*O. nerka*) salmon and juvenile Atka mackerel (*Pleurogrammus monopterygius*). We studied interannual variability in feeding habits, zooplankton prey fields, diel feeding chronology and diet overlap in the deepwater regions of the western Bering Sea in September–October, 2002–2004. Pacific salmon and Atka mackerel fed primarily on zooplankton. Most of their diets consisted of few food items. All fish showed similar diel feeding rhythms and consumed food mostly during the day. Diet overlaps were high for small- and medium-size salmon and moderate for large salmon. We conclude there was a low potential for feeding competition among major salmon species and juvenile Atka mackerel in the western Bering Sea in fall 2002–2004.

Keywords: pink salmon, chum salmon, sockeye salmon, Atka mackerel, salmon diet, diet overlap, western Bering Sea

INTRODUCTION

In the last decade the abundance and percentage in nekton of the some Asian Pacific salmon stocks have increased (Temnykh et al. 2004). These fish are one of the dominant species in the upper epipelagic zone (0–50 m) of the western Bering Sea. Juvenile Atka mackerel (*Pleurogrammus monopterygius*) also forage at these depths in the water column. In fact, the biomass of Atka mackerel in some years is comparable with the biomass of abundant salmon species.

Increased salmon abundance may be related to their food supply. Some recent studies have suggested the possibility that a limitation of food resources and/or the carrying capacity of the epipelagic zone can affect Pacific salmon (Azumaya and Ishida 2000; Klovatch 2000; Kaeriyama 2003). Alternatively, other studies have concluded that salmon do not exhaust the carrying capacity of epipelagic ecosystems (Shuntov and Temnykh 2004; Dulepova et al. 2005).

In this work we describe feeding habits of all size-classes of chum (*Oncorhynchus keta*) and sockeye (*O. nerka*) salmon as well as juvenile pink salmon (*O. gorbuscha*) and juvenile Atka mackerel. We compare zooplankton prey fields, diel feeding chronology and diet overlap of these fish in order to determine their food supply and the potential for feeding competition among them.

MATERIALS AND METHODS

The study was based on data collected as part of epipelagic surveys by TINRO-Centre in deepwater regions (Komandor Basin and western Aleutian Basin) of the western Bering Sea in September–October, 2002–2004 (Fig. 1). All surveys were conducted by the R/V *TINRO*. During the surveys trawl tows in the surface layer were conducted over 24-h periods. The vertical spread of the trawl was 31–41 m, depending on the towing speed. The trawl was usually towed for one hour at about 4.6 kts.

Stomach contents were analyzed aboard the vessel using the method described by Chuchukalo and Volkov (1986). Stomachs were removed from up to 25 fish of each size-class (10–30, 31–40, 41–50, 51–60 cm) at each station. Stomach contents of each size-class of fish were mixed and weighed. Prey composition was determined to the lowest possible taxonomic category and the percentage of each prey item was estimated visually. The total number of stations and stomachs analyzed were: pink salmon – 100/1255, chum salmon – 297/2469, sockeye salmon – 292/1836, Atka mackerel – 41/671.

Stomach content indices (SCI) were determined to standardize for differences in body size. SCI is the prey weight•10,000/body weight (‰₀₀) (we multiply the index by 10,000 for easy reading). The relationship between time of day and SCI of fish was approximated by a fourth-order
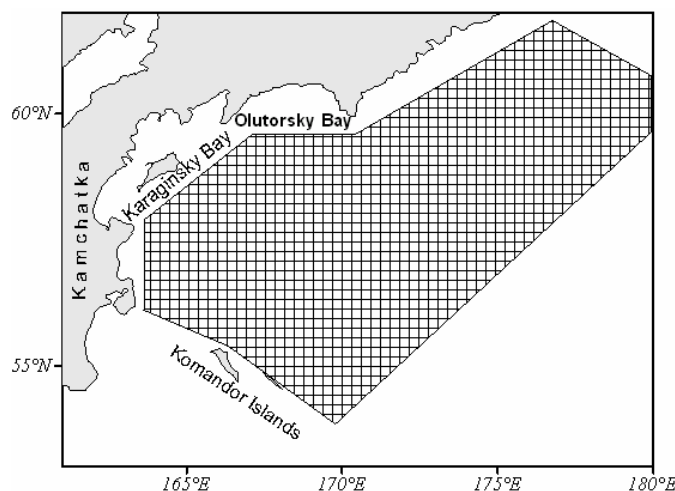
Fig. 1. Regions and stations for collecting pink, chum and sockeye salmon and Atka mackerel in the western Bering Sea in fall 2002–2004.

polynomial. Daily rations were estimated using the method of Kogan (1963) and Novikova (1949). Daily ration was equal to the sum of food consumed food at each time period (% body weight). Diet overlap was evaluated only for co-occurring fish. Two fish were considered to be co-occurring if they were caught together. This approach allows us to exclude the influence of spatial segregation on our conclusions on the potential for feeding competition between fish.

Feeding similarity indices were calculated using the formula of Schoener (1970):

$$C_{xy} = 1 - 0.5 \sum (\mid p_x - p_y \mid)$$

where C_{xy} is the feeding similarity index of species x and y, and p is the fraction of each prey item in the diet of species x and y.

Zooplankton samples were collected in a Jedy net with a 0.1 m² mouth opening and a 0.168-mm mesh net. Tows were conducted from 50 m depth to the surface. Plankton samples were sorted and counted aboard the vessel using the method of Volkov et al. (2004). Because salmon and Atka mackerel ingested primarily large zooplankton (> 3 mm), zooplankton biomass was evaluated for items > 3 mm. To estimate zooplankton biomass we used corrective catchability coefficients: for euphausiids, mysids and chaetognaths < 10 mm = 2, 10–20 mm = 5, > 20 mm = 10; for hyperiid amphipods < 5 mm = 1.5, 5–10 mm = 3, > 10 mm = 5; for copepods < 5 mm = 2, > 5 mm = 3; for polychaetes, small jellyfish and other slow-moving animals = 1.

RESULTS AND DISCUSSION

Copepods and chaetognaths dominated the zooplankton in fall 2002–2004 (Table 1). These taxa comprised 75–90% of the overall zooplankton biomass. The total proportion of euphausiids, hyperiid amphipods and pteropods was rela-

Table 1. Average densities (mg/m³) of the dominant zooplankton categories in the upper epipelagic zone of the western Bering Sea in fall 2002–2004.

	2002		2003		2004	
	mg/m³	%	mg/m³	%	mg/m³	%
Copepoda						
Neocalanus plumchrus	702.1	55.3	207.0	26.6	23.7	4.9
Eucalanus bungii	36.2	2.8	42.3	5.4	14.3	3.0
Other Copepoda	20.7	1.6	38.0	4.9	35.2	7.3
Euphausiacea						
Thysanoessa longipes	30.1	2.4	49.1	6.3	54.5	11.3
T. inermis	12.5	1.0	2.5	0.3	10.7	2.2
Other Euphausiacea	10.3	0.8	3.5	0.5	14.7	3.0
Amphipoda						
Themisto pacifica	16.9	1.3	24.2	3.1	18.8	3.9
Other Amphipoda	0.2	< 0.1	0.1	< 0.1	0.6	0.1
Pteropoda						
Clione limacina	0.2	< 0.1	9.3	1.2	< 0.1	< 0.1
Limacina helicina	0.4	< 0.1	11.7	1.5	2.0	0.4
Chaetognatha	388.7	30.6	350.2	45.0	287.5	59.6
Decapoda	2.0	0.2	1.4	0.2	2.6	0.5
Cnidaria						
Aglantha digitale	49.3	3.9	31.7	4.1	14.7	3.0
Other Cnidaria	0.3	< 0.1	1.6	0.2	-	-
Other	0.5	< 0.1	6.1	0.8	3.3	0.7
Total	1270.5	100	778.7	100	482.4	100
Sample Size	48	-	42	-	39	-

tively low: 6% in 2002, 13% in 2003 and 21% in 2004. The density of the predominant copepod *Neocalanus plumchrus* decreased sharply from 2002 to 2004, resulting in a decrease in total zooplankton biomass. In contrast, the euphausiid density (mainly *Thysanoessa longipes*) increased from 2002 to 2004. Nevertheless, the proportion of *T. longipes* was consistently low, never exceeding 12%. In 2003, the pteropod biomass was much higher than in 2002 and 2004.

In fall 2002–2004, most of the diets of juvenile pink, chum and sockeye salmon consisted of two prey items – the hyperiid amphipod *Themisto pacifica* and the euphausiid *Thysanoessa longipes*, except in 2003, when *T. longipes* was replaced by the pteropod *Limacina helicina* (Fig. 2). Prey composition for juvenile Atka mackerel was similar to that for juvenile salmon, but the fraction contributed by the copepod *Neocalanus plumchrus* was higher.

Diets of adult chum and sockeye salmon also consisted of few prey items. The three prevalent food items of chum and sockeye salmon constituted 56–77% and 65–92% of the diet, respectively. In 2002 and 2004, the hyperiid amphipod *Themisto pacifica*, the euphausiid *Thysanoessa longipes* and fish (juvenile Atka mackerel, walleye pollock *Theragra chalcogramma*, and myctophids *Stenobrachius leucopsarus* and *S. nannochir*) were the dominant prey (Fig. 3). Small nektonic organisms became more important in the diet of larger fish. In fall 2003, the adult salmon stomachs con-

tained mostly pteropods and small squids. Chum salmon fed almost exclusively on the pteropod *Clione limacina*, and sockeye salmon fed mainly on small squids, the pteropod *L. helicina* and the amphipod *Themisto pacifica*. Probably, the high proportion of pteropods in the salmon diet is related to the increasing biomass of *C. limacina* and *L. helicina* (Table 1). It is important to note that the above-mentioned plankton species are much less abundant in the upper epipelagic zone than are copepods and chaetognaths (Table 1).

All fish showed similar diel feeding rhythms, especially juveniles (Fig. 4). Maximum stomach fullness occurred from the afternoon to midnight and decreased from night to morning (see Efimkin et al. 2004; Volkov and Kosenok this volume).

Co-occurring juvenile salmon diets were similar. Schoener's diet similarity indices varied from 0.58 to 0.95 (Table 2). Similarity of diets of Atka mackerel and juvenile salmon was lower (0.27–0.59), mainly because copepods were a
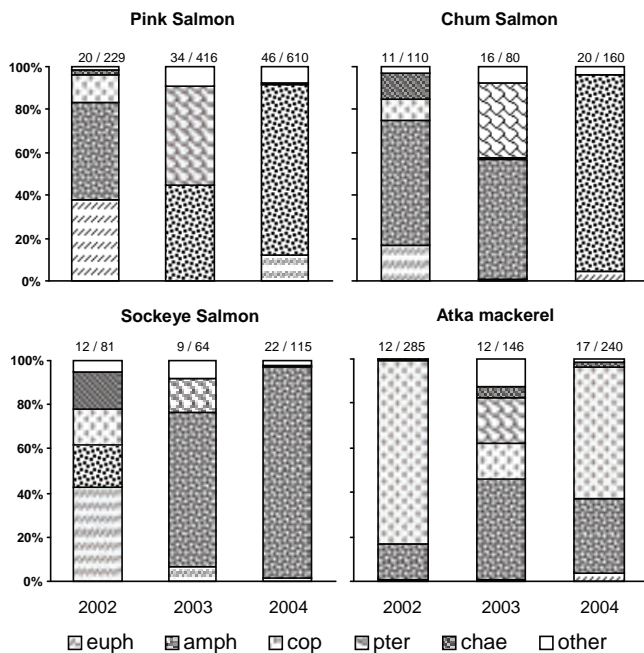
Fig. 2. Percent composition of major prey collected from juvenile pink, chum and sockeye salmon and Atka mackerel stomachs in the western Bering Sea in fall 2002–2004. Number of stations and stomachs analysed are shown above each column. euph = euphausiids, amph = amphipods, cop = copepods, pter = pteropods, chae = chaetognaths.
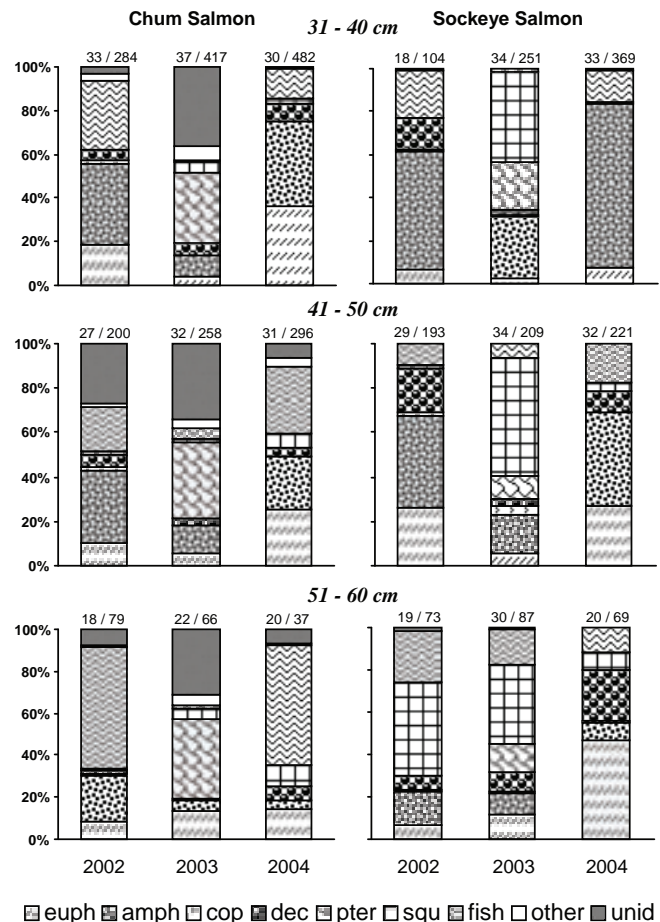
Fig. 3. Percent composition of major prey collected from adult chum and sockeye salmon stomachs by fish size group in the western Bering Sea in fall 2002–2004. Number of stations and stomachs analysed are shown above each column. euph = euphausiids, amph = amphipods, cop = copepods, dec = decapods, pter = pteropods, squ = squid, unid = unidentified.
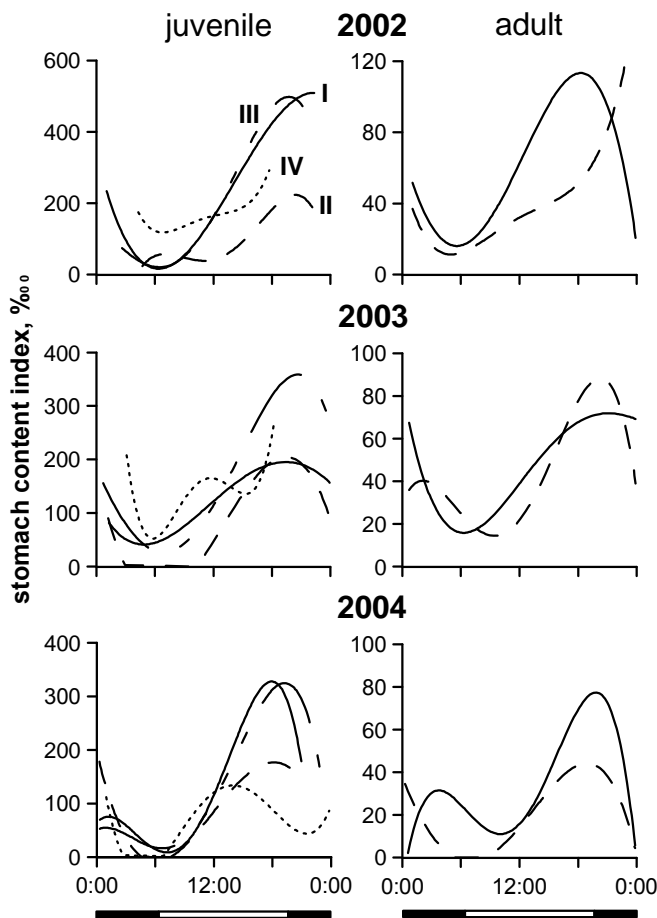
Fig. 4. The relationship between time of day and stomach content index (polynomial trends) of chum (I), sockeye (II) and pink (III) salmon and Atka mackerel (IV). Black bars at bottom of graphs indicate darkness.

more important prey item for Atka mackerel.

Diet similarity of co-occurring adult chum and sockeye salmon was the highest for fish 31–40 cm body length, decreasing for larger fish (Table 3). Similarity of diets was lower (0.21–0.26) only in 2003 as a result of chum feeding on pteropods and of sockeye feeding on squids. In 2003, Pacific salmon were very abundant in the western Bering Sea (Shuntov and Temnykh 2004). Despite this high abundance, daily rations of chum and sockeye salmon in 2002, 2003 and 2004 were similar (Table 4). This may be explained by plasticity in salmon feeding and/or the presence of sufficient food resources in the upper epipelagic zone of the western Bering Sea.

In summary, we report that chum, pink and sockeye salmon and Atka mackerel feed on few food items (mainly two or three species). The fractions of plankton in these diets were low. There were either no or very few chaetognaths in any diet. There was only weak feeding specialization. Feeding rhythms of fish were stable and similar but feeding similarity indices were high. Our results suggest that there was a low potential for feeding competition among major salmon species and juvenile Atka mackerel in the western Bering Sea in fall 2002–2004.

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Table 2. Diet similarity of co-occurring juvenile pink, chum and sockeye salmon and Atka mackerel in the western Bering Sea in fall 2002–2004. Subscripts are station numbers.

Species	2002			2003			2004		
	Pink	Chum	Sockeye	Pink	Chum	Sockeye	Pink	Chum	Sockeye
Pink	1			1			1		
Chum	0.87_8	1		0.88_{11}	1		0.75_{16}	1	
Sockeye	0.69_{10}	0.58_9	1	0.70_8	0.72_7	1	0.88_{19}	0.95_{12}	1
Atka mack.	-	-	-	0.52_8	0.27_2	-	0.43_{14}	0.53_7	0.59_5

Table 3. Diet similarity of co-occurring adult chum and sockeye salmon in the western Bering Sea in fall 2002–2004. Subscripts are station numbers.

	Sockeye								
	31–40 cm			41–50 cm			51–60 cm		
	2002	2003	2004	2002	2003	2004	2002	2003	2004
Chum	0.81_{13}	0.21_{28}	0.53_{24}	0.54_{24}	0.26_{26}	0.78_{26}	0.42_{14}	0.21_{17}	0.39_8

Table 4. Daily rations of chum and sockeye salmon in the western Bering Sea in fall 2002–2004.

Size group (cm)	2002	2003	2004
Chum Salmon			
10–20	7.5	7.0	7.9
30–40	4.6	3.9	2.1
40–50	3.8	3.9	2.4
50–60	4.5	3.8	3.2
Sockeye Salmon			
20–30	4.7	6.0	6.0
30–40	2.8	4.8	3.2
40–50	1.8	3.6	2.8
50–60	1.8	3.8	1.0

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Wounding of Pacific Salmon in Relation to Spatio-Temporal Variation in Distribution Patterns of Important Predatory Fishes in the Russian Economic Zone

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Abstract: Variation in distribution patterns of major predatory fishes in the Russian economic zone was analyzed using Pacific Scientific Research Fisheries Center (TINRO-Centre) archival trawl survey data for 1980–2004. Species analyzed include *Alepisaurus ferox*, *Anotopterus nikparini*, *Lamna ditropis*, *Lampetra tridentata*, *L. camtschatica*, *Prionace glauca*, *Somniosus pacificus* and *Squalus acanthias*. Our data show that there is strong geographic variation in the relative abundance of predatory fishes. Differences in predator abundance were noted among large-scale geographical units (Bering, Okhotsk and Japan seas and adjacent waters of the North Pacific Ocean) and small-scale geographical units (shelf, continental slope, and deep-water basins; the upper epipelagic layer, lower epipelagic layer, upper mesopelagic layer, lower mesopelagic layer). We conclude that the rate of occurrence of Pacific salmon injuries was species-, age- and region-specific. This implies that it is necessary to consider species, age and region when estimating predator-related mortality of Pacific salmon.

Keywords: predator-prey interaction, spatial structure, spatial overlap, distribution pattern, vertical distribution, marine mortality, crosscovariance

INTRODUCTION

Research on the spatio-temporal interaction between Pacific salmon and their predators is important for studying natural mortality of Pacific salmon as indicated by the number of publications on this topic (Beamish et al. 1992; Radchenko 1994; Shuntov 1994; Nakano and Nagasawa 1996; Nagasawa 1998a, among others). In the majority of these studies the influence of only one predator is considered. Estimates of various predators' contribution to Pacific salmon natural mortality are difficult to obtain because it is not known what percentage of Pacific salmon survives attacks by particular predators. Low levels of occurrence of injured individuals in catches may result from either low attack rates or low rates of survival after attacks.

Studies are needed to understand relationships between the occurrence of certain injuries and Pacific salmon mortality. Previous studies suggest that spatial overlap between prey and predators is often a direct measure of predation intensity (Fahrig et al. 1993; Radchenko 1994; Melnikov 1997; Savinykh and Glebov 2003, among others). In our study we focused on the quantifying degree of spatial overlap between Pacific salmon and their predators.

MATERIALS AND METHODS

Data from the Pacific Scientific Research Fisheries Center (TINRO-Centre) research pelagic trawl surveys for 1980–2004 (2914 stations in the Bering Sea, 6056 in the Sea of Okhotsk, 2164 in the Japan Sea and 7105 in the northwestern Pacific Ocean) were used to identify the distribution of Pacific salmon (*Oncorhynchus gorbuscha*, *O. keta*, *O. kisutch*, *O. nerka* and *O. tschawytscha*) and their predators. Species analyzed include North Pacific daggertooth (*Anotopterus nikparini*), longnose lancetfish (*Alepisaurus ferox*), Pacific lamprey (*Lampetra tridentata*), Arctic lamprey (*L. camtschatica*), salmon shark (*Lamna ditropis*), spiny dogfish (*Squalus acanthias*), blue shark (*Prionace glauca*) and Pacific sleeper shark (*Somniosus pacificus*). These species have been identified as the most intensive consumers of Pacific salmon during the marine phase of their life history (Parin 1968; Jones and Geen 1977; Nagasawa and Kaeriyama 1995; Sviridov et al. 2004, among others). Wounding and scarring of Pacific salmon were analyzed based on data from four epipelagic trawl surveys by TINRO-Centre in the western Bering Sea and adjacent Pacific waters (summer surveys - from July 15 to August 24, 2003, and from June 6 to July 17, 2004; autumn surveys - from September 14 to

October 25, 2003, and from September 11 to October 23, 2004). We recorded the presence or absence of each type of injury for every Pacific salmon examined. The analysis was performed separately for every life-history stage: juvenile (age .0), immature (age .1 and older) and maturing (individuals that will spawn in the current season). Subsamples for biological analysis were taken randomly to enable us to extrapolate toward total catch. We calculated the average percentage of individuals with injuries by each predator for each survey. In order to calculate the average percentage of individuals with injuries by each predator for each survey we weighted the percentage of a certain injury at a particular station by CPUE values at that station. This is standard procedure to adjust for the contribution of individual trawl tows to the outcome of an analysis by weighting them in proportion to the values of CPUE. As a result trawl tows with high CPUE have had a greater influence upon calculated average values, as compared to tows with low CPUE. The type of injury was determined based on its external appearance according to published descriptions (Beamish 1980; Welch et al. 1991; Shuntov et al. 1993; Radchenko and Semenchenko 1996; Melnikov 1997; Balanov and Radchenko 1998; Kukuev 1998; Savinykh and Glebov 2003). Based on these sources, injuries by a particular predator can be summarized as follows: injuries by North Pacific daggertooth are slashes or cuts, which are located only on one side of the body. The other side of the body has a series of very small stab-wounds or hard-to-observe superficial scratches made by the needle-like teeth on the lower jaw. Slashes are made by large daggers in the North Pacific daggertooth's upper jaw. Injuries by longnose lancetfish are usually located on both sides of the body, unlike North Pacific daggertooth injuries. Lamprey wounds on Pacific salmon vary from circular depressions to longitudinal gouges with a loss of scales at the edges of the wound.

We used a three-dimensional scatterplot to identify predatory fish distributions. During this analysis we considered average values for depth of species occurrence (distance between the sea surface and the middle of the trawl mouth weighted by CPUE), depth at the location of trawling (distance between the sea surface and the sea bottom, weighted by CPUE) and relative biomass. In addition we conducted interspecific cluster analysis on similarities in spatial distribution patterns of Pacific salmon and their predators during the summer in the upper epipelagic layer. For the cluster analysis we used the matrix of Pearson correlation coefficients for relationships between different pairs of species' relative biomass averaged for every 1 x 1 degree cell in Tables 1 and 2 the upper epipelagic layer.

To analyze the adaptive significance of spatio-temporal distributions of major predatory fish species in relation to Pacific salmon we used a traditional geostatistical technique - crosscovariance analysis (Isaaks and Srivastava 1989; Cressie 1993; Goovaerts 1997; Johnston et al. 2003). Crosscovariance is a statistical tendency of variables to vary in ways that are related to each other. Positive crosscovariance

Table 1. Average percentage of Pacific salmon with injuries by lamprey, North Pacific daggertooth or longnose lancetfish in the western Bering Sea and North Pacific Ocean during summer 2003 (July 15 to August 24), autumn 2003 (September 14 to October 25), summer 2004 (June 6 to July 17; Northwest Pacific only), and autumn 2004 (September 11 to October 23). J = Juvenile; Imm = Immature; Mat = maturing fish.

Survey		Pink salmon		Chum salmon			Coho salmon		Sockeye salmon			Chinook salmon		
		J	Mat	J	Imm	Mat	J	Imm	J	Imm	Mat	J	Imm	Mat
Lamprey														
2003	summer		0.5	0	0.1	0.2		10.0	0.0	0.4	0		1.2	
	autumn	0		0	0.5	1.0	0		0.3	0.5		0	1.3	
2004	summer		0.4		0	0.3		0		0.0	0		0	100.0
	autumn	0		0.2	0.4	0.0	0.9	0	0	1.1		0	0	
North Pacific daggertooth														
2003	summer		9.5	0	2.4	6.0		0	0	1.7	16.7		1.3	
	autumn	0.7			4.3	2.0	0		1.9	2.7		2.3	1.3	
2004	summer		3.8		6.3	9.7		6.7		5.4	14.3		5.6	0
	autumn	0.1		0.2	2.9	11.8	0	33.3	0	1.4		0	2.0	
Longnose lancetfish														
2003	summer		0.9	0	0	0		0	0	0.1	0		0.2	
	autumn	0		0	0.2	0	0		0	0.3		0	1.3	
2004	summer		0.1		0	1.3		0		0.0	3.6		0	0
	autumn	0		0	0.2	0	0	33.3	0	0.0		0	0	

Table 2. Average CPUE (number of individulas per km²) and total abundance (TA in thousand metric tonnes) of predatory fishes in the western Bering Sea and North Pacific Ocean during summer 2003 (July 15 to August 24), autumn 2003 (September 14 to October 25), summer 2004 (June 6 to July 17; Northwest Pacific only), and autumn 2004 (September 11 to October 23).

Survey	Arctic lamprey		Pacific lamprey		North Pacific daggertooth		Longnose lancetfish	
	CPUE	TA	CPUE	TA	CPUE	TA	CPUE	TA
2003 summer	1.45	0.09	37.11	1.04	1.54	1.73		
autumn	0.72	0.09	6.82	1.04	0.57	0.47	0.10	0.43
2004 summer			0.80	0.23	3.39	2.88	1.11	2.54
autumn			3.49	0.37	0.65	0.40		

occurs when both variables tend to be above their respective means together, and negative crosscovariance occurs if one variable tends to be above its mean when the other variable is below its mean. We restricted our analysis to the following characteristics: relative abundance of maturing pink and chum salmon and North Pacific daggertooth, and percentage of individual salmon with injuries by North Pacific daggertooth.

RESULTS

The average percentages of individuals with injuries by each predator for each survey are provided in Table 1. Based on their external appearance, the majority of injuries were classified as caused by North Pacific daggertooth. The incidence of injuries by lampreys was lower, and the injuries attributed to longnose lancetfish predation were lowest. The incidence of individuals with lamprey injuries was quite low for Pacific salmon. The highest injury rate was seen in maturing individuals. Due to the lower abundance of Arctic lamprey (compared with Pacific lamprey) in the Bering Sea (Table 1, 2) it can be expected that the latter species is a greater cause of Pacific salmon mortality. Archival trawl survey data analysis has shown that the abundance of Arctic lamprey in the northwestern Pacific was much lower compared to the abundance of Pacific lamprey (Figs. 1 and 2).

Pacific lamprey abundance in the northwestern Pacific was quite low compared to the levels in the Bering Sea (Fig. 2). This was associated with lower rates of injury by lamprey in the northwestern Pacific (Table 1). The abundance of Arctic lamprey decreased by half from summer to autumn of 2003 but we did not observe a decrease in injury rates. Moreover, in some species we observed an increase in rates of injury by lampreys later in the year. The same situation was noted for Pacific lamprey. The trawl survey data showed that the abundance of North Pacific daggertooth in the Bering Sea was several times lower than in the northwestern Pacific both in summer and autumn (Figs. 3 and 4). This may explain the lower injury rates in the Bering Sea (Table 1). Maturing pink and chum exhibited unexpectedly low injury rates in the northwestern Pacific. The abundance of daggertooth decreased by almost 50% from summer to autumn (Table 2). However, the rate of injury rose in some species (immature chum, sockeye and chinook) (Table 1). Maturing Pacific salmon were the most intensely wounded by daggertooth (Table 1).

Latitudinal variation in occurrence of individuals injured by North Pacific daggertooth was evident in a statistically significant ($P < 0.05$) negative correlation between the latitude of the trawling location and the percentage of salmon injured by North Pacific daggertooth. This was observed for immature chum and sockeye salmon during two surveys in the northwestern Bering Sea (the summer survey from July 15 to August 24, 2003, and the autumn survey from September 14 to October 25, 2003) (Fig. 5). During summer, North Pacific daggertooth migrate northward to the central Bering Sea, but its main concentrations are located in the Pacific waters off the Kuril Islands (Figs. 3 and 4). The northward decrease in proportion of individuals injured by North Pacific daggertooth, which was observed earlier by Savinykh and Glebov (2003) for chinook and coho salmon in the waters off the Kuril Islands, can also be explained by these migrations.

Juvenile salmon exhibited much lower rates of North Pacific daggertooth injuries compared with immature and maturing fish (Table 1). This may be the result of a lower number of attacks, or lower survival after attacks, or both. There is no doubt that the percentage of individuals that die immediately after North Pacific daggertooth attacks is much higher in juveniles compared with immature and maturing fish. The higher rates of injury in the more abundant salmon species compared with less abundant species are unlikely to be explained by higher survival rates. We hypothesize that daggertooth may forage more intensively on dominant salmon species. Such a concentration of predation on dominant prey species is consistent with the foundations of optimal foraging theory.

The abundance of longnose lancetfish was significantly lower than that of the North Pacific daggertooth (Table 1). Similar to daggertooth, the longnose lancetfish was most abundant in southern regions during summer–autumn (Figs. 6 and 7). The longnose lancetfish injuries were highest on maturing individuals (coho, sockeye, and chum) (Table 1). It is possible that this may be due to the lower survival of smaller individuals compared with larger ones. However, it

Fig. 1. Arctic lamprey CPUE (kg/km²) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.
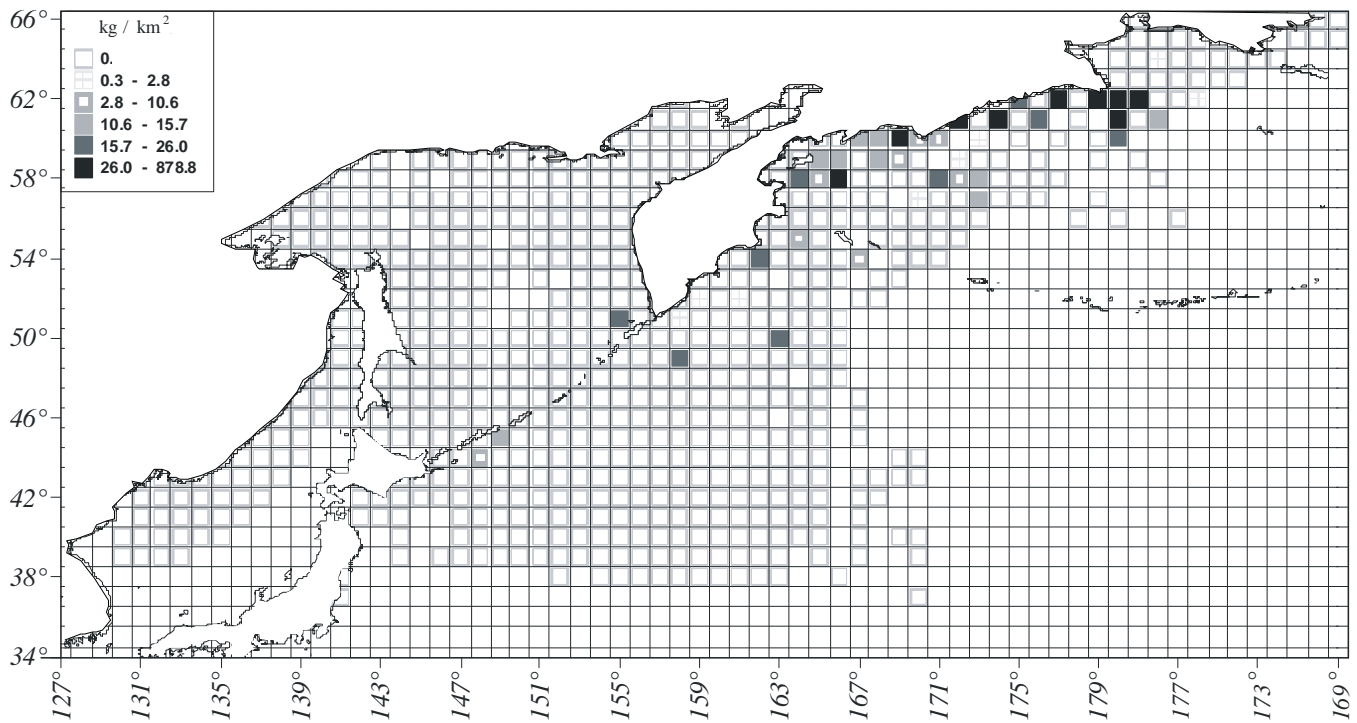
Fig. 2. Pacific lamprey CPUE (kg/km²) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.
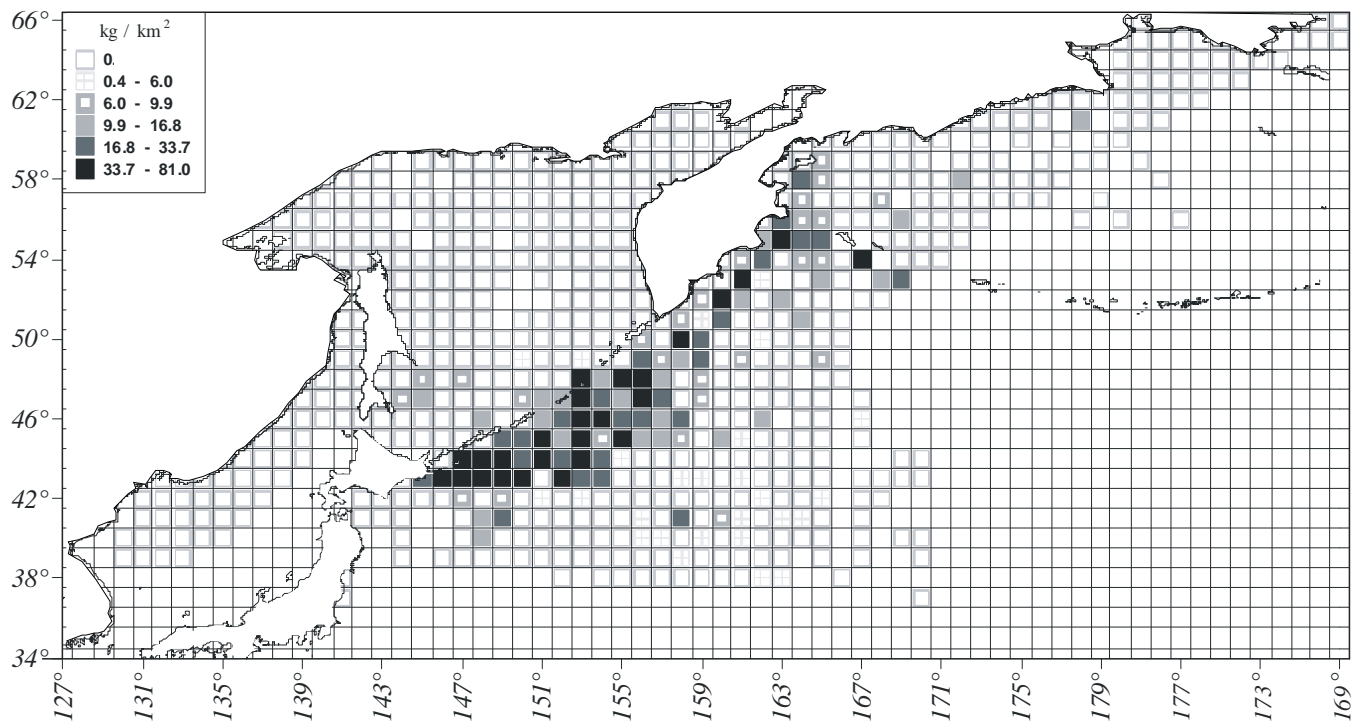
Fig. 3. North Pacific daggertooth CPUE (kg/km²) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.
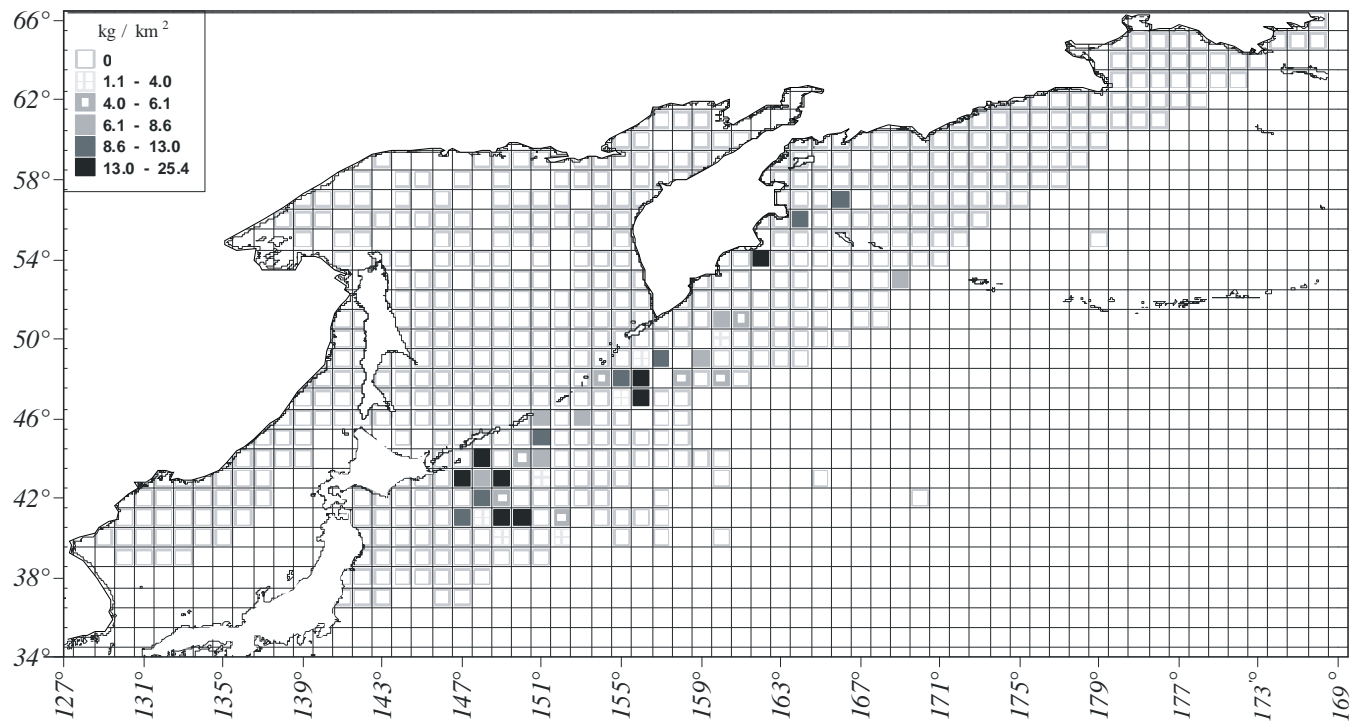
Fig. 4. North Pacific daggertooth CPUE (kg/km²) in the upper epipelagic layer of the northwest Pacific and adjacent areas during autumn. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.
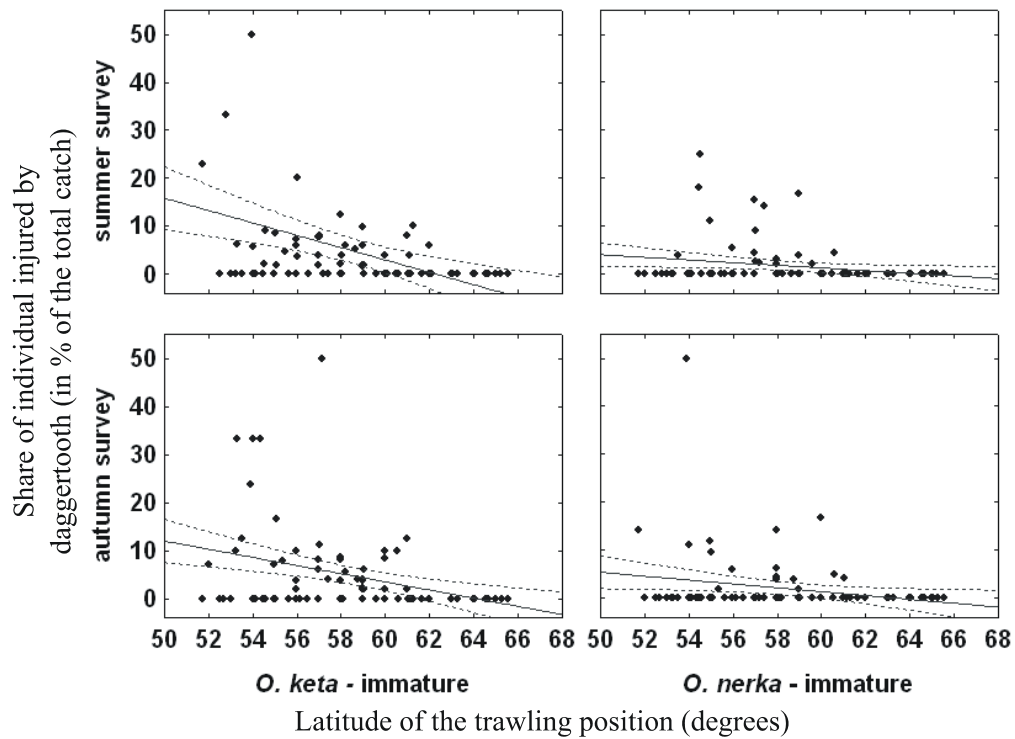
Fig. 5. The relationship between the latitude of the trawling location and the percentage of individuals injured by North Pacific daggertooth (% of total catch) during two surveys in the northwestern Bering Sea (summer survey from July 15 to August 24, 2003 and autumn survey from September 14 to October 25, 2003). Solid and dotted lines indicate trends and 95% confidence interval of the trend lines, respectively.

Fig. 6. Longnose lancetfish CPUE (kg/km²) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.

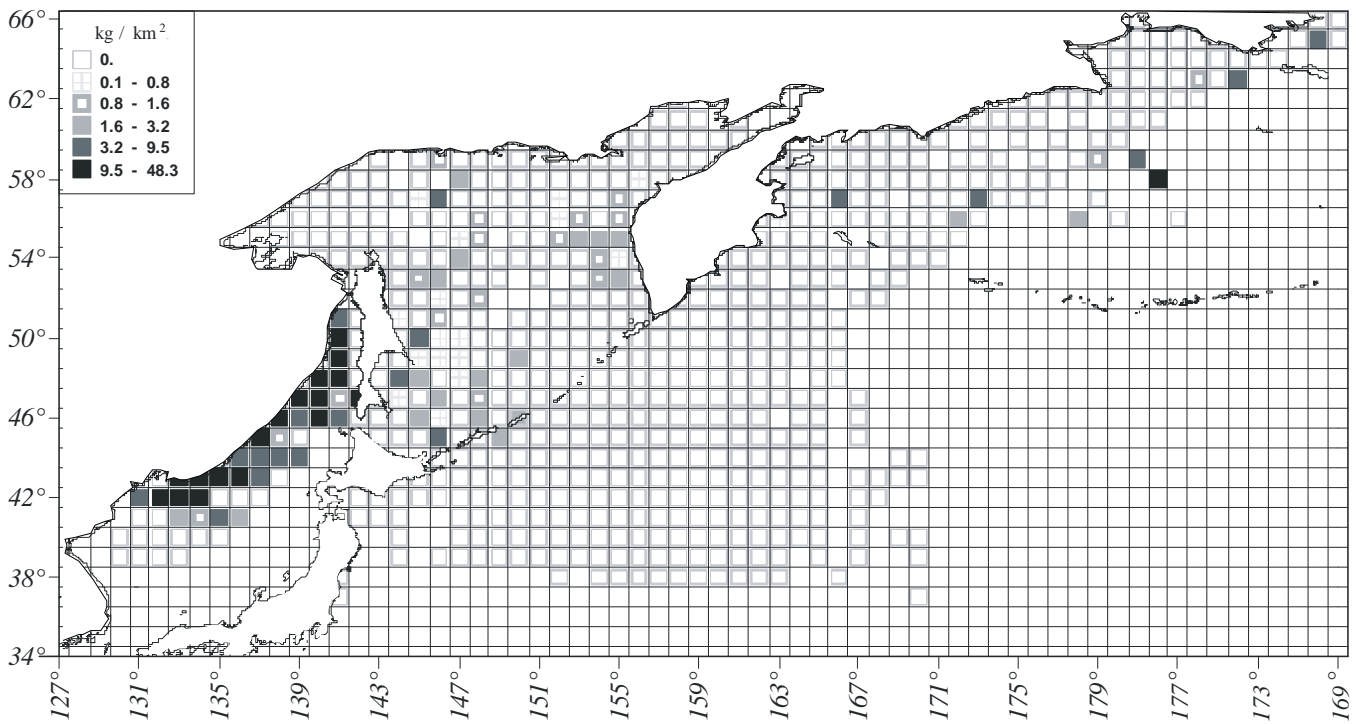**Fig. 7.** Longnose lancetfish CPUE (kg/km²) in the upper epipelagic layer of the northwest Pacific and adjacent areas during autumn. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.
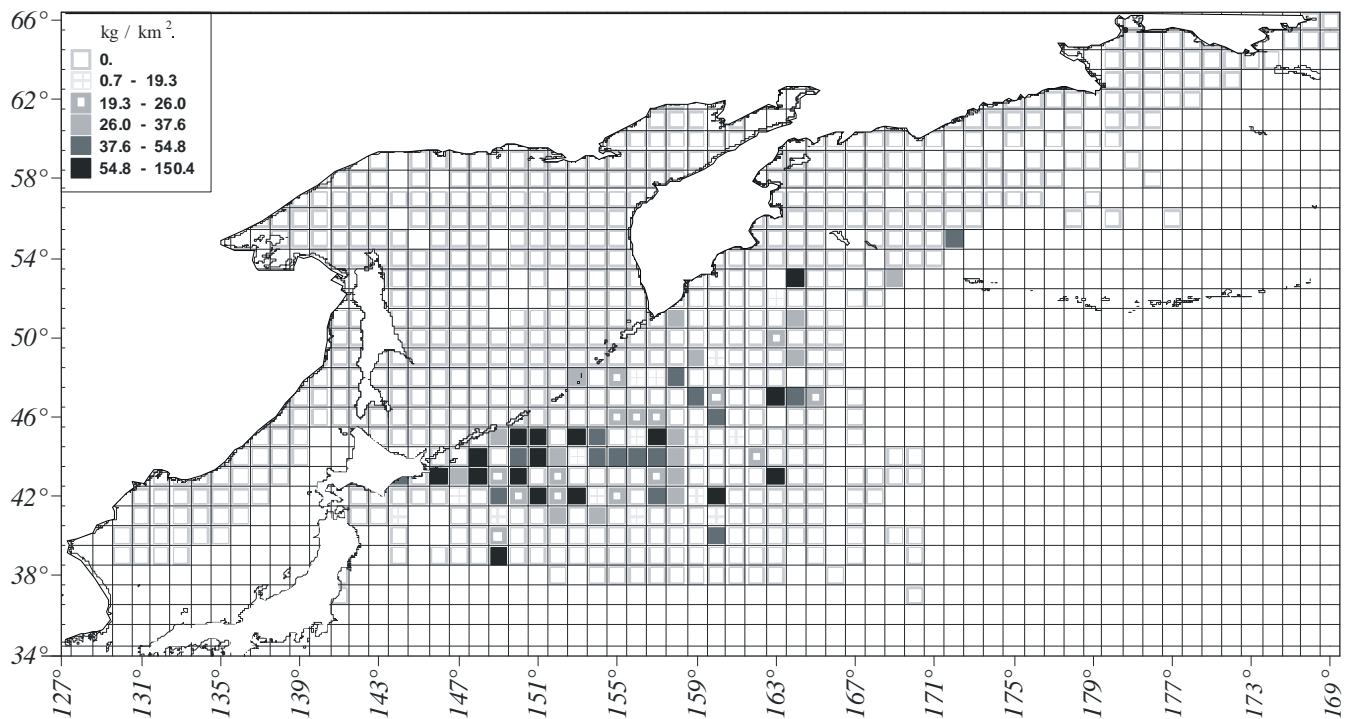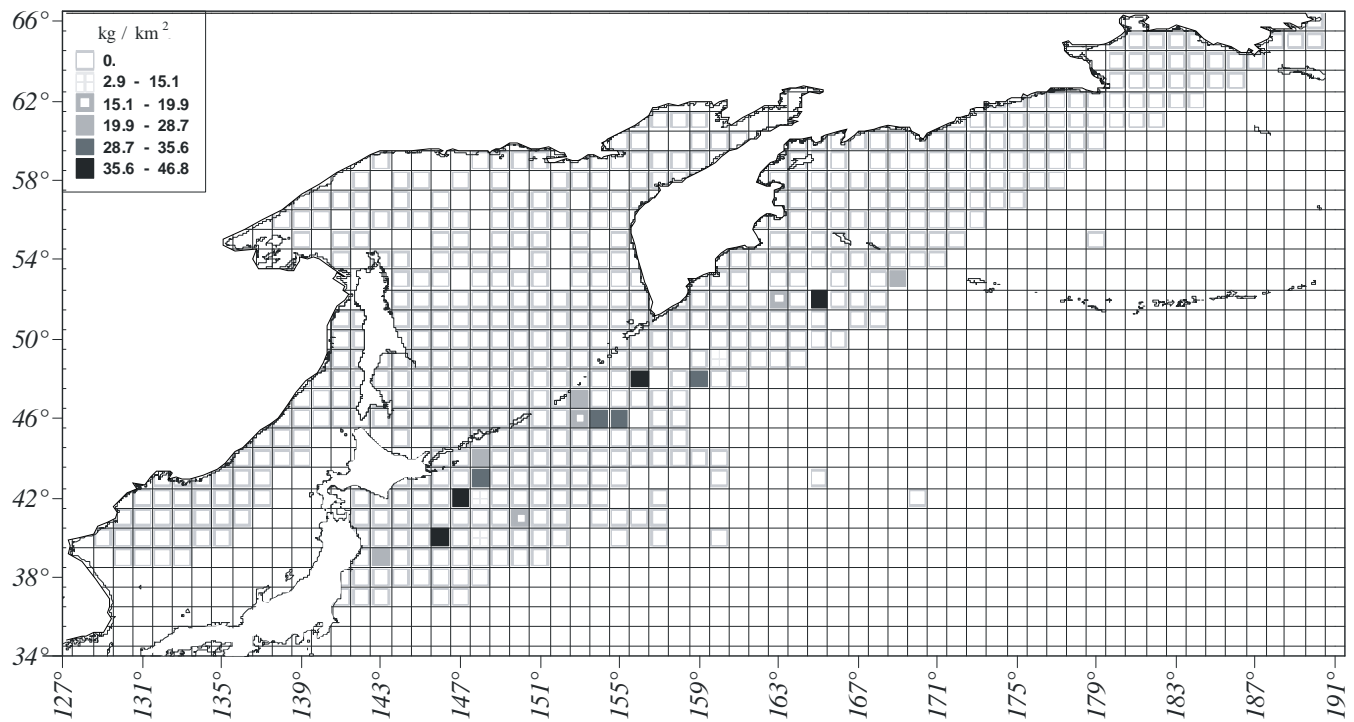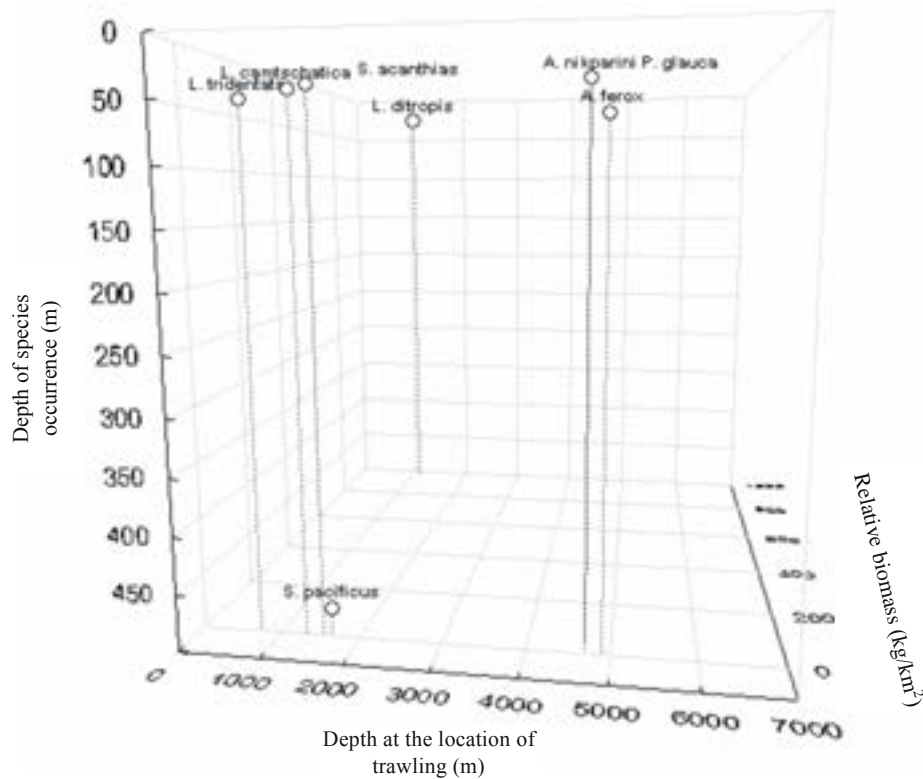

Fig. 8. Interspecific differences in the relationship between average depth at the location of trawling, depth of species occurrence, and relative biomass for different predatory fish during the summer.

could also result from the higher survival of larger fish. A certain accumulation of non-fatal injuries with age may also occur.

The incidence of injuries by longnose lancetfish on salmon were several times lower compared to those caused by daggertooth (Table 1). This may be due either to the lower abundance of longnose lancetfish, or to the higher mortality rate caused by lancetfish attacks.

Injuries by sea mammals were rarely observed during the surveys. It is known that sea mammal attacks, as well as attacks by sharks, are more lethal to salmon than those of the North Pacific daggertooth (Melnikov 1997). This may explain the almost complete absence of salmon with injuries by sea mammals and sharks in our samples. In addition, sea mammals attack Pacific salmon mainly in the coastal zone (Melnikov 1997), which was not included in our surveys.

The three-dimensional scatterplot that we used to identify predatory fish distributions showed that during the summer, which is the period of highest abundance of predatory fish species in the Russian economic zone, three distinct groups of species can be discerned (Fig. 8). The first group includes North Pacific daggertooth, longnose lancetfish and blue shark, living primarily in upper epipelagic layer over deepwater basins. The second group includes Arctic lamprey, Pacific lamprey, spiny dogfish and salmon shark, living primarily in upper epipelagic layer over the continental slope. Salmon sharks had biomass values that significantly exceeded those of other predatory fish. The third group included only Pacific sleeper sharks that live primarily in the mesopelagic layer over the continental slope.

Results of interspecific cluster analysis on similarity in spatial distribution patterns of Pacific salmon and their predators during summer in the upper epipelagic layer are shown in Fig. 9. They are quite different from the results shown in Fig. 8. This is understandable if we keep in mind that during cluster analysis the main emphasis is put not upon environmental preferences, but upon the similarities in small-scale (1 x 1 degree cells) spatial distributions. For instance, the two species of lamprey that lived in similar habitats (Fig. 8) fell into distinct clusters (Fig. 9). This corresponded well with the significant differences in spatial distribution of Pacific and Arctic lampreys (Figs. 3 and 4).

Maps of species spatial distributions revealed that during summer the spatial structure of the North Pacific daggertooth was characterized by relatively higher overlap with maturing pink salmon compared with large chum (Figs. 3, 10 and 11).

Geostatistical analysis of spatio-temporal distributions of major predatory fish species in relation to Pacific salmon revealed the following. The relative abundance of maturing pink salmon exhibited positive crosscovariance with the relative abundance of North Pacific daggertooth at relatively small separation distances, while at relatively large separation distances crosscovariance was negative (Fig. 12). In other words, the locations with relatively high values of

maturing pink salmon abundance were characterized by relatively high North Pacific daggertooth abundance. The crosscovariance between large maturing and immature chum salmon (fork length > 30 cm) and North Pacific daggertooth was opposite to that observed for maturing pink salmon. Large chum salmon exhibited negative crosscovariance with the relative abundance of North Pacific daggertooth at relatively small separation distances, while at relatively large separation distances crosscovariance was positive (Fig. 12). This can be explained if we keep in mind that majority of large chum salmon were located in the Bering Sea (Fig. 11), which is quite distant from the major concentrations of North Pacific daggertooth (Fig. 3). Maturing pink salmon had a distribution similar to that of the North Pacific daggertooth (Fig. 10).

During the prespawning migration of maturing chum salmon in the northwest Pacific in the summer 2004 survey, there was significant spatial overlap with North Pacific daggertooth. This was evident from the positive crosscovariance values at small separation distances between the relative abundance of maturing chum salmon and North Pacific daggertooth. As a result, the relationship between crosscovariance and separation distance was negative (r = -0.48, p = 0.01).

No statistically significant relationship was observed between separation distance and crosscovariance between the relative abundance of North Pacific daggertooth and the percentage of maturing chum salmon with injuries during the summer 2004 survey. As with maturing chum salmon, no similarity in spatial distribution was observed between North Pacific daggertooth and the percentage of maturing pink salmon with injuries in the catch. This means that the spatial distribution of injured maturing pink and chum salmon was independent of the North Pacific daggertooth distribution in the northwest Pacific during summer 2004. This might be explained by the dispersal of injured individuals away from the places where they were injured.

SUMMARY

Our analysis showed that relative abundance of predatory fishes shows strong geographic variation. Spatial structure of predatory fish species is an indirect but functionally informative indicator of predation intensity. Information on when and where a particular predator is most abundant may reveal locations and time periods when Pacific salmon are most vulnerable.

Quite often the abiotic (temperature, depth, e.g.) preferences of Pacific salmon and their predators differ significantly. In this sense the predator's spatial structure is often a tradeoff between an optimal abiotic environment and better feeding conditions. For instance, the spatial distribution of North Pacific daggertooth is mostly restricted to southern, warmer areas of the northwest Pacific, whereas the majority of Pacific salmon are located in more northern, cooler
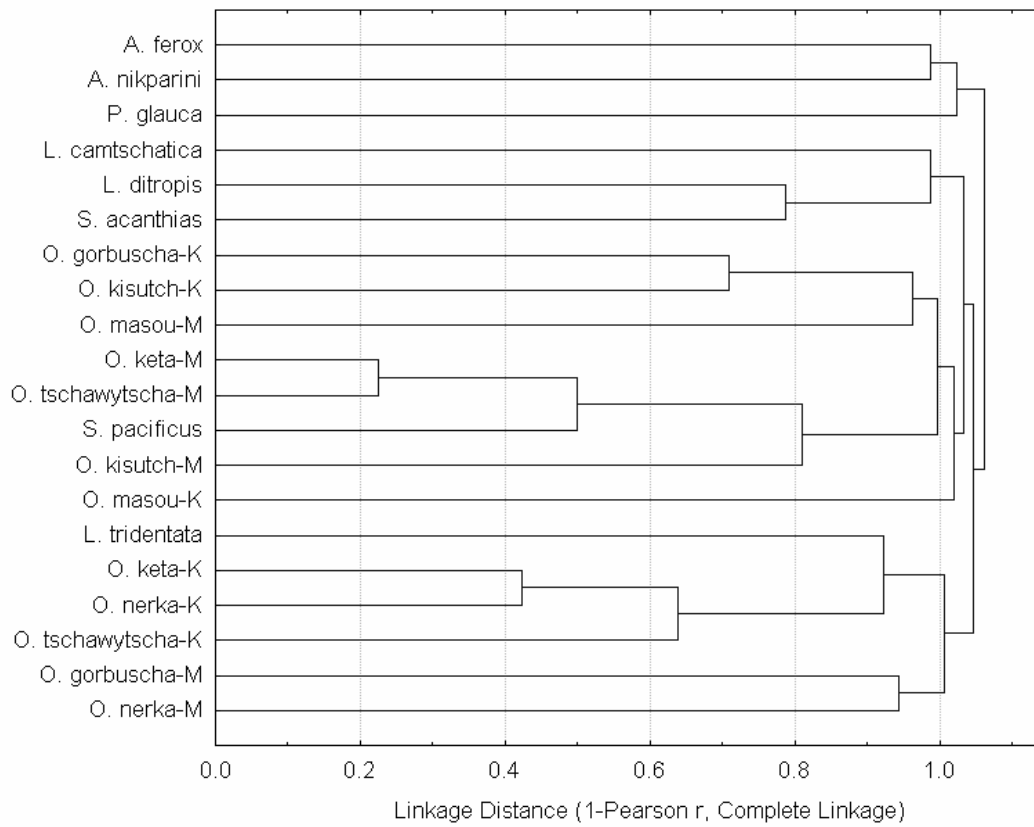
Fig. 9. Results of interspecific cluster analysis on similarity in spatial distribution patterns of Pacific salmon and their predators during summer in the upper epipelagic layer. The cluster analysis is based on matrix of Pearson correlation coefficients for relationship between different pairs of species relative biomasses averaged for every 1x1 degree cell sampled in the upper epipelagic layer.
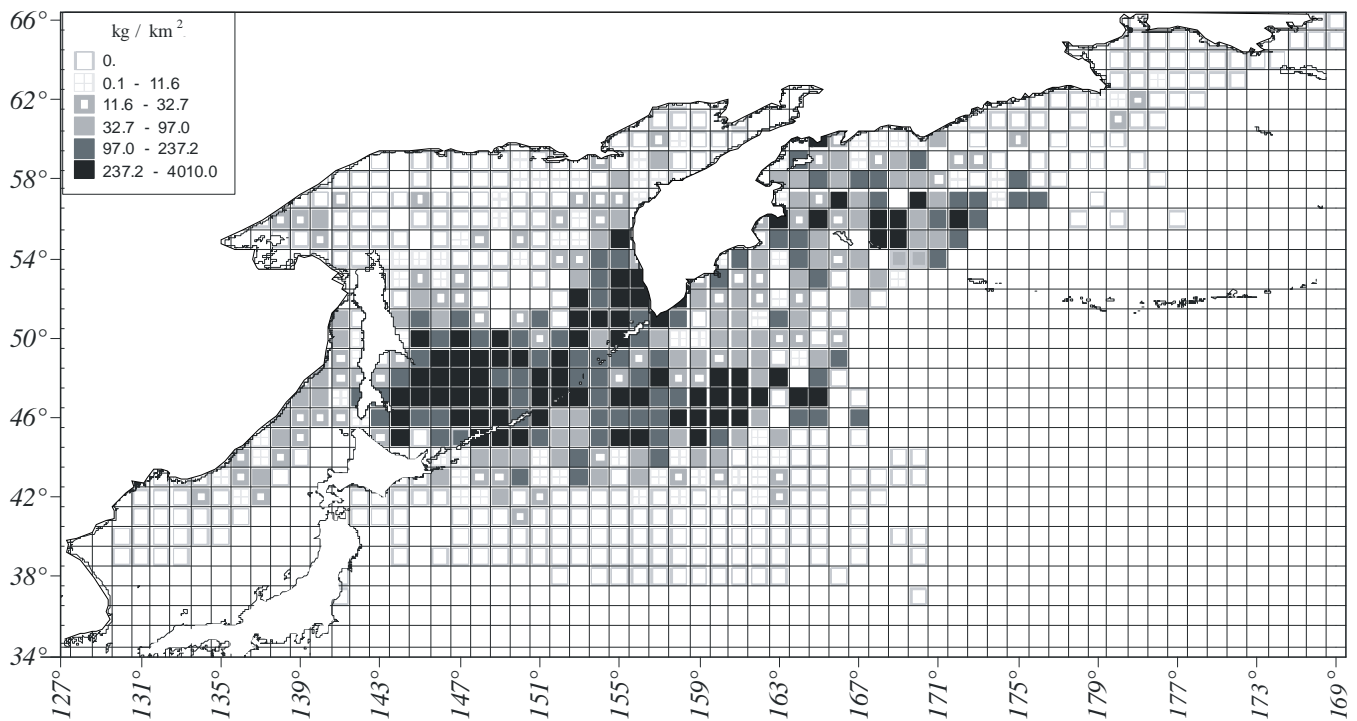
Fig. 10. Maturing pink salmon CPUE (kg/km²) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.
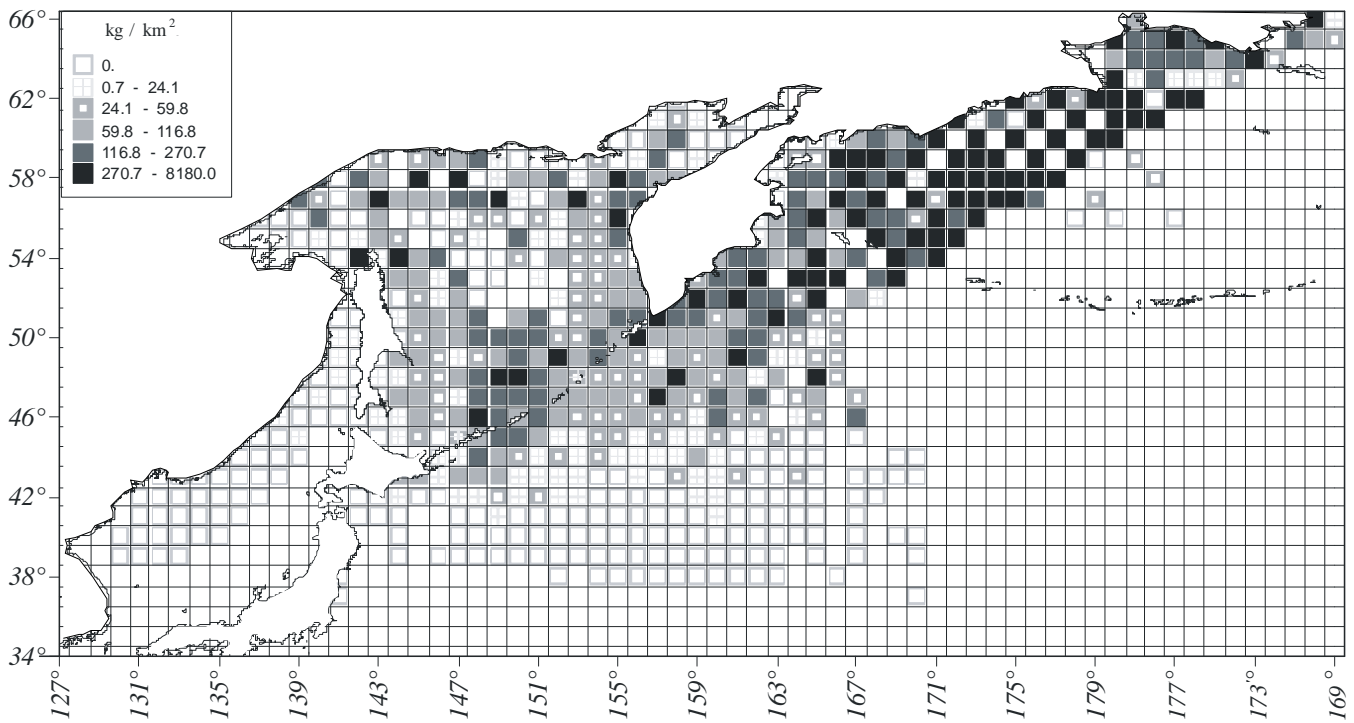
Fig. 11. Large maturing and immature (fork length > 30 cm) chum salmon CPUE (kg/km) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.
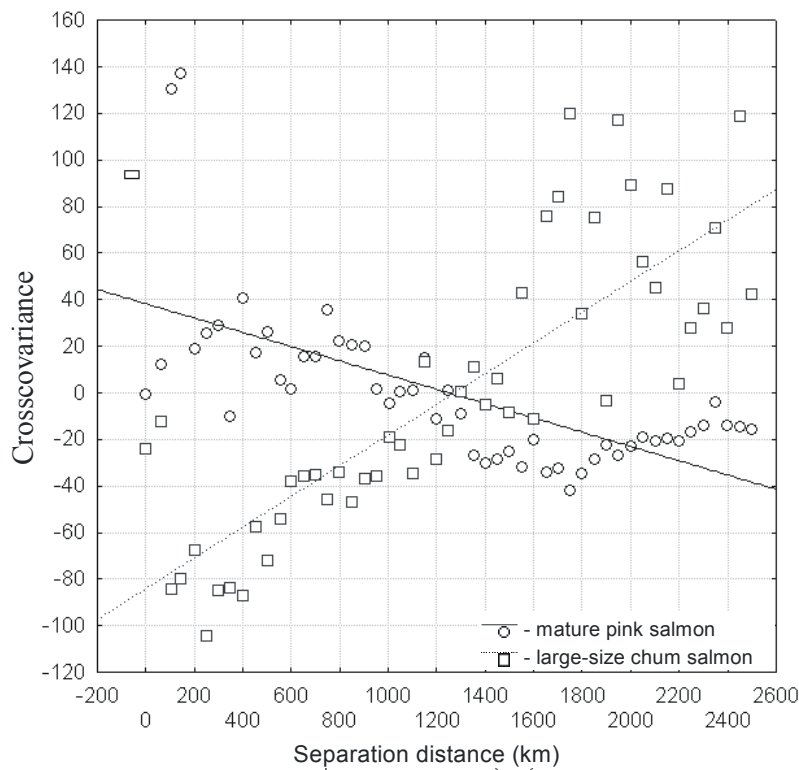
Fig. 12. Relationship between separation distance and crosscovariance between relative abundance of North Pacific daggertooth and relative abundance of: a) maturing pink salmon (circles and solid line; r = -0.66, p < 0.001), b) large maturing and immature (fork length > 30 cm) chum salmon (squares and dotted line; r = 0.83, p < 0.001). Analysis is based upon relative abundance values in every 1x1 degree cell sampled in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer, 1980–2004.

regions (Melnikov 1997).

Our data testify for species, age, seasonal and geographic specificity in rates of injury of Pacific salmon. This implies the necessity of considering species, age and regional specificity when estimating predator-related mortality of Pacific salmon. The spatio-temporal interaction between Pacific salmon and predatory fishes is complex. It is not simply the product of predator versus prey abundance levels.

Based on datasets of the 2002–2004 surveys in the Bering Sea and northwest Pacific we considered the spatial variability in injuries of Pacific salmon. We observed significant spatial aggregation in the levels of occurrence of Pacific salmon wounding. During both surveys the number of individuals injured by North Pacific daggertooth was greater in the southern, deepwater areas than in the northern, shallower waters. This pattern agrees both with our data on the higher abundance of North Pacific daggertooth in the Pacific waters off the Commander Islands and southwestern regions of the Bering Sea, compared with northern areas of the Bering Sea.

A review of the data on the occurrence of injuries has shown that, probably, maturing Pacific salmon in summer–autumn are somehow more susceptible to daggertooth attacks, compared with fish at other stages of maturity. Another possible explanation for the increased percentage of injured maturing individuals is that a certain accumulation of non-fatal injuries may occur as fish get older.

Previous studies suggest that spatial overlap between prey and predators is often a direct measure of predation intensity (Fahrig et al. 1993; Radchenko 1994; Melnikov 1997; Savinykh and Glebov 2003, among others).

In this study, spatial distribution of injured salmon was not a good indicator of the spatial allocation of predation intensity. This implies that spatial occurrence of injured Pacific salmon should be treated carefully in the context of the predator-prey relationship.

Most mathematical descriptions of predator-prey interactions fail to take into account the spatio-temporal structures of populations, which can lead to errors or misinterpretations (De Angelis and Petersen 2001). For instance, a compact pulse of prey migrating through a field of quasi-stationary predators may not be well described by standard predator-prey models, because the predators and prey are unlikely to be well mixed. The prey may be exposed to only a fraction of the predator population at a time. This underscores the importance of properly accounting for the 'ecological neighborhood', or effective feeding range, of predators in models.

If the home ranges of predators are relatively small, the predators could have significantly less effect than they would if they were sufficiently mobile to mix quickly through the entire reservoir and continue their individual contacts with the prey pulse for the entire time of prey passage (De Angelis and Petersen 2001). Thus, modelers dealing with the problem of predation on migrating populations need to take the

feeding range of the predator into account.

Studies characterizing horizontal predator–prey spatial overlap in marine species have documented that at small scales prey distribution is relatively uniform and predator–prey overlap is often poor (Rose and Leggett 1990; O'Driscoll et al. 2000; De Robertis 2002). Spatial overlap between Atlantic cod and capelin has been well studied over a range of scales. At large scales (> 4–20 km) cod exhibit positive overlap with capelin, their primary prey, but the distributions become negatively correlated at smaller scales (< 2–10 km). Planktivorous seabirds overlap poorly with zooplankton at scales < 2.5 km where prey distribution is relatively uniform, but exhibit consistent overlap at larger spatial scales where zooplankton biomass is more variable (Logerwell et al. 1998; De Robertis 2002). Our data on Pacific salmon and the distribution of predatory fish species has a resolution of approximately 30–60 naut mi due to survey grid spacing. Further studies at smaller spatial scales are desirable to explain spatial interactions of Pacific salmon and their predators. As the references cited above imply, it may be that at smaller spatial scales (< 30 naut mi) spatial interaction of Pacific salmon and their predators will differ.

Temporal variation in production processes, density-dependent habitat selection and the resulting changes in spatial structure of Pacific salmon and their predators, can affect Pacific salmon predation through changes in predator-prey spatial overlap. Predation intensity is likely to increase during periods of lower Pacific salmon abundance and increased abundance and geographic range of their predators. To achieve better understanding of Pacific salmon predation-related mortality we need to accumulate long-term data series. However, estimates of various predators' contributions to Pacific salmon natural mortality are greatly impeded by the fact that at present there are no data on how scarring and wounding relates to mortality. Without this information all estimates of Pacific salmon mortality will be indirect and rough approximations.

ACKNOWLEDGEMENTS

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Wounding of Pacific Salmon by Predators in Gillnet Catches in the Russian Economic Zone in 2004

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Abstract: We describe data on wounds, scars, and marks on Pacific salmon caught during a gillnet survey by the R/V *Ecopacific* in the northwest North Pacific Ocean and southwest Bering Sea in summer–fall 2004. A classification scheme to systematize visual observations of various types of wounds caused by two major predator groups (piscivorous fish and seals) is suggested. Three general trends in the results apply to all species of salmon caught in gillnets during their prespawning migrations. First, wounding by fish and seals does not depend on salmon body size at either the intra- or inter-specific level. Second, the highest percentage of wounds were caused by seals and two piscivorous species, longnose lancetfish and North Pacific daggertooth (25–47% of wounds in North Pacific waters adjacent to Kamchatka). The percentage of wounds caused by lampreys was relatively low. Third, the percentage of healed wounds (scars) in mature salmon increased at the end of the prespawning migration, indicating that the energy expended to regenerate injured tissues may delay maturation. It was difficult to distinguish between natural wounds, which occurred before salmon were caught, and artificial wounds, which occurred after salmon were caught, particularly because of the length of fishing operations (~10 hr) and the ready availability of gillnet-caught salmon to predators. The results, however, can be used an indicator of general background conditions that influence natural predation of salmon during their prespawning migrations in the open ocean.

Keywords: salmon, gillnet, marine, predators, wounds, prespawning migration, Russia

INTRODUCTION

Assessment of the marine survival of Pacific salmon (*Oncorhynchus* spp.) is one of most important steps in forecasting the abundance of adult returns to spawning grounds. Accurate estimates of marine survival would significantly improve scientifically applied measures used to regulate commercial fisheries. Complexity in salmon stock assessments results primarily from the multi-factor character of salmon survival over the course of their ocean feeding migrations, as documented in numerous scientific publications. It is well known that the mechanisms of most abiotic and biotic processes influencing marine mortality cannot be controlled. The marine survival of Pacific salmon can fluctuate extensively, which, in turn, directly influences the quality of run forecasts. Contemporary research on this problem usually involves studies that provide information on various factors that may influence survival at different levels of salmon ecological interactions.

The results reported in this paper are also just one stage in the study of prey-predator interactions of Pacific salmon in the ocean. There are already many publications that provide insight into the variety (types) of wounds, scars, and marks caused by predators, as well as the effects of these wounds on the survival of salmon at different ocean

life stages (Birman 1950; Sano 1960; Makhnyr' and Perlov 1988; Welch et al. 1991; Shuntov et al. 1993a,b; Radchenko and Semenchenko 1996; Melnikov 1997; Balanov and Radchenko 1998; Grishina 2000; Kaplanova and Zolotukhin 2002; Savinykh and Glebov 2003; Sviridov et al. 2004). Most of these studies, however, are species-specific and illustrate the influence of only a single predator. This is understandable because wider information is often limited, especially concerning information on the life histories of predators, particularly because the predators themselves are usually not the target of any marine fisheries.

Nevertheless, the need for data on the amounts and the rates of salmon removal by predators during their ocean feeding or prespawning migrations is urgent. Some observations have provided insight into the percentage of Pacific salmon consumed by different species of piscivorous fishes and marine mammals at sea (Sobolevsky 1983; Burkanov et al. 1991; Shuntov et al. 1993a,b; Melnykov 1997; Aschepkov and Radchenko 2000). Moreover, there are a number of local assessments of the effects of some pinnipeds on the abundance of particular salmon stocks during their prespawning migrations (Makhnyr' and Perlov 1988; Grishina 2000; Makoedov et al. 2000). The problem of prey-predator interactions is understandably much broader, concerning not only marine stages of Pacific salmon but also freshwa-

ter stages, when juvenile and adult survival is influenced not only by fishes and pinnipeds, but also by birds, bears, and other mammals. Unfortunately, most existing assessments of the influences of predators on salmon survival are in the nature of expert opinions, rather than applied-scientific methods for management of Pacific salmon resources in the Russian Far East. This problem can be solved only through complex studies, involving collaboration with specialists from various fields of science.

In this paper, we evaluate the effects of marine predators on salmon in gillnet catches in the open ocean. Traumas (wounds, scars, and marks) on Pacific salmon were observed and analyzed in fish caught in the northwest North Pacific Ocean and southwest Bering Sea during summer and fall 2004. Similar observations have been carried out by KamchatNIRO scientists during gillnet cruises since the mid 1990s. Nevertheless, all historical records of this research were brief, i.e., often one-word descriptions such as "bite", without further reliable identification and description of the characteristics of the wound. Therefore, we decided to develop a new method for systematizing field records of these observations based on data collected in 2004. In addition, we planned to develop a standard method of monitoring marine predators of Pacific salmon. Identification and assessment of wounds, scars, and marks on salmon are complex. There are always chances for error, especially in the identification of the species of predator that caused the wound. We took this problem into account during our work by classifying wounds to a higher taxonomic category, which reduced the possibility of mistaken identification of potential predators.

The objectives of our study were to develop a classification scheme for field identification of wounds caused by marine predators of Pacific salmon, and to use data from gillnet catches in 2004 to determine the incidence of wounded salmon in gillnet catches during their prespawning migrations.

MATERIALS AND METHODS

Materials for this study were collected from June to September 2004 during gillnet research by KamchatNIRO scientists aboard the R/V *Ecopacific*. The research was carried out primarily in the northwest North Pacific Ocean (North Pacific waters adjacent to Kamchatka), where there were 27 salmon gillnet operations, and less extensively in the southwestern Bering Sea, where there were 4 gillnet operations (Fig. 1). All salmon caught by research (control) gillnets (square mesh size 55 mm; 20–30 nets per each diurnal operation) were analyzed. The length of one net was 50 m. Each fishing operation lasted 10 hours. In total, 2,202 Pacific salmon were examined, including 699 sockeye (*O. nerka*), 529 chum (*O. keta*), 714 pink (*O. gorbuscha*), 110 chinook (*O. tshawytscha*), and 150 coho (*O. kisutch*) salmon.

The character of wounds, scars, and marks on each salmon was recorded during shipboard processing of speci-
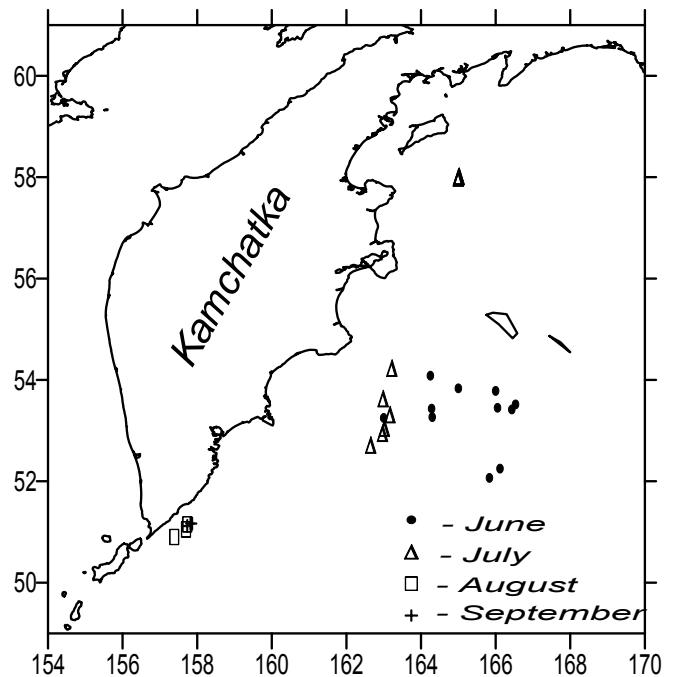
Fig. 1. Study area and locations of gillnet stations during the R/V *Ecopacific* survey of Pacific salmon in the northwest North Pacific Ocean and southwest Bering Sea in June–September 2004.

mens; afterward the possible predator that caused the wound was recorded. Wounds were identified either by referring to published data on the effects of different predators on Pacific salmon or by our own direct observations. All illustrative materials in this document were collected during our studies, except for materials by Sano (1960), that illustrate wounds caused by salmon sharks. We were not able to photograph salmon shark bites, because only one salmon with this type of wound was observed, even though salmon sharks were caught frequently in our nets.

RESULTS AND DISCUSSION

Identification of Wounds

Illustrations and descriptions of the different types of wounds classified in this document are shown in Fig. 2 and Table 1. The wounds of Pacific salmon were classified by division into two principal types. Type I wounds are those caused by fish or fish-like species, and include three subtypes: I–a longnose lancetfish (*Alepisaurus ferox*) and North Pacific daggertooth (*Anotopterus nikparini*), I–b lamprey and I–c salmon shark (*Lamna ditropis*). Type II wounds are those caused by seals (Pinnipedia). Our classification scheme provides only a general assessment of wounds on salmon caused by piscivorous fishes and seals. Additional work is needed to reliably identify predators to a particular species or group of species with similar hunting behavior and functional morphology.
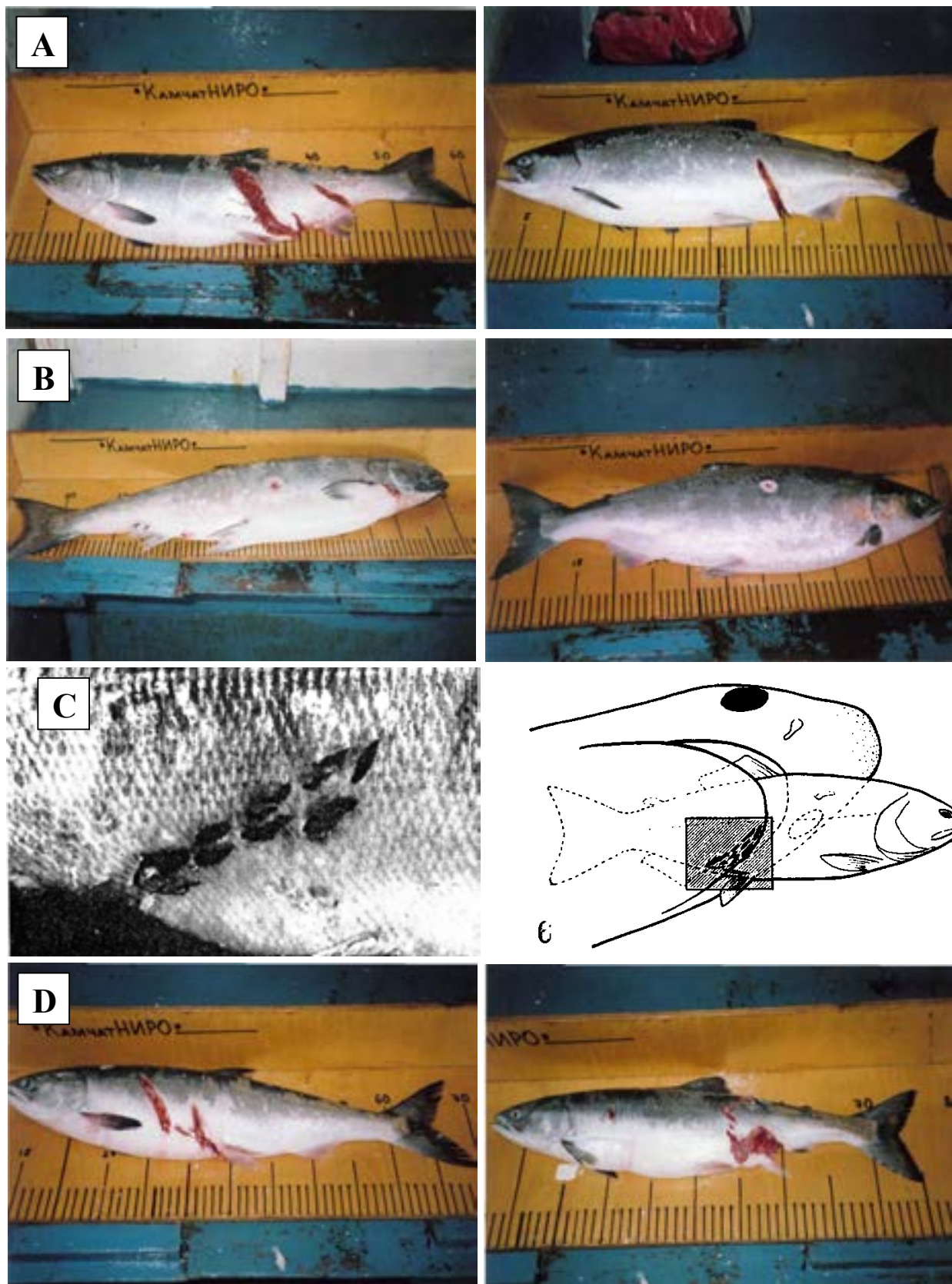
Fig. 2. Examples of the types of wounds caused by marine fish and mammal predators of Pacific salmon. (A) Type I – a (fish): lancetfish and daggertooth; (B) Type I – b (fish): lamprey; (C) Type I – c (fish): salmon shark (Sano, 1960); (D) Type II : seals.

Table 1. Classification scheme and description of characteristics of wounds on Pacific salmon.

Type of wounds	Predator	Characteristics of wounds
Type I (fish)	a) Lancetfish , daggertooth	Transversal cuts of various depths occur on one side of the fish, usually directed at a backward slanting angle to the vertical axis of fish. On the other side of the body, small lacerated wounds can be observed as a prolongation of a main cut. These wounds are most frequent in the area of anal fin.
	b) Lamprey	The wound has a precise, rounded shape. In superficial wounds, diagnostic marks made by lamprey teeth can be observed. In serious wounds, there is a deep round hole that exudes semi-digested tissues.
	c) Salmon shark	Obvious marks or puncture wounds caused by placoid shark teeth. Characteristically, the bite has multiple rows of teeth marks.
Type II	Seals (Pinnipedia)	Lacerated wounds bearing the marks of pinniped canine or incisor teeth. As a rule, the wounds are deep, with tissues pulled out. Parallel scratches (pinniped claw rake abrasions) are frequently observed.

The wounds caused by longnose lancetfish and North Pacific daggertooth, which have similar hunting behavior, were combined into one group because reliable identification of species did not seem possible. The bites of these two species can possibly be differentiated by measuring the depth of the wound on the side opposite from the main cut site because longnose lancetfish have bigger teeth on the lower jaw than North Pacific daggertooth. To some extent, however, species identification from such measurements are unreliable because the shape and depth of the wounds correlate directly with the size and speed of movement of prey, as well as the size and the angle of attack of the predator. Despite these problems, many researchers have concluded that these types of wounds are caused only by North Pacific daggertooth (Welch et al. 1991; Radchenko and Semenchenko 1996; Melnykov 1997; Balanov and Radchenko 1998; Savinykh and Glebov 2003). Our criticism of this method does not pertain to well-documented incidents, e.g., when a daggertooth was taken from a net with its teeth inside a salmon. The origin of a bite in such a case is not in question, however, we assume that such cases are quite rare. There are published assessments of salmon wounds in which the bites of longnose lancetfish and North Pacific daggertooth were not differentiated by species (Shuntov et al. 1993a, b).

In most studies, identification of species of predators from wounds, scars, and marks on salmon has relied heavily on the subjective perceptions of scientists and field technicians. Thus, some errors are likely. In support of our suggestion to combine the assessment of wounds caused by longnose lancetfish and North Pacific daggertooth, we note that in 2004 longnose lancetfish were observed more frequently than North Pacific daggertooth in the bycatch of the R/V *Ecopacific* commercial nets (65-mm mesh). This may be related to the large size of longnose lancetfish (up to 5–7 kg); it is also possible that a large proportion of smaller daggertooth may have escaped the 65-mm mesh nets. We cannot provide reliable information on the dynamics of catches of these piscivorous fishes, however, because no data were recorded on these species in the catches of control nets (55-mm mesh). Although our information from commercial catches is anec-

dotal, longnose lancetfish and daggertooth are known to feed actively in the waters of the North Pacific Ocean adjacent to Kamchatka and the Kuril Islands, and their estimated biomass from trawl surveys in this region is as high as 2,000 tonnes (Shuntov et al. 1993a, b; Melnikov 1997).

Among the lampreys, three species occur in the Far Eastern section of the Russian Economic Zone: Pacific lamprey (*Entosphenus tridentatus)*, Arctic lamprey (*Lethenteron camtschaticum)* and far eastern brook lamprey (*L. reissneri)*, according to the revised classification (Moiseev and Tokranov 2000). We classified all wounds, marks, and scars made by these species as "lamprey" because identification to species from the number of teeth was not possible. This problem was primarily due to the effects of the digestive enzymes of lamprey, which masked the traces of teeth marks. Nevertheless, among all species of lamprey mentioned the Arctic lamprey is the most significant predator of salmon in our study area.

The salmon shark is one of the most active predators of Pacific salmon in the North Pacific Ocean. In most cases, however, a salmon shark attack results in the death of the salmon before it can be caught in a net, e.g., during our cruise we caught only one salmon with a shark bite.

Among pinnipeds the most active consumers of Pacific salmon in this region are spotted seals (*Phoca larga*), Bering ringed seals (*P. hispida krasheninnikovi*), and Okhotsk Sea ringed seals (*P. hispida ochotensis*) of the family Phocidae, and Northern fur seals (*Callorhinus ursinus*) and Steller sea lions (*Eumetopias jubatus*) of the family Otariidae. The percentage of salmon in the diets of pinniped species varies and depends on the time of year. During their prespawning period, salmon become readily available to seals and sea lions in areas along traditional marine migration routes where salmon concentrations are highest. Accordingly, the wounding of Pacific salmon in gillnet catches by pinnipeds can be very significant.

Northern fur seals are probably the most important cause of wounding of salmon in gillnets, as indicated by our multiple observations of their behavior during gillnet retrieval. Fur seals were observed stealing and eating salmon directly

Table 2. The incidence (% of N) of mature Pacific salmon in gillnet catches with wounds caused by some species of predators. N = number of fish.

Species	Region	Period in 2004	CPUE (fish/ tan)	N	Mature in catch (%)	Length (cm)	Incidence of wounds (%)				Total incidence (%)
							Type I (fish)			Type II (seal)	
							a	b	c		
Sockeye	Northwest Pacific Ocean	June 11-29	1.44	188	95	57.4	3.2	0.5	0.5	7.4	11.6
		July 8-18	4.88	102	50	55.8	4.9	0	0	12.7	17.6
		August 16-21	2.47	19	21	57.0	5.3	0	0	10.5	15.8
		September 12-14	6.50	-	-	-	-	-	-	-	-
		Average	3.8	309	42	56.7	3.4	0.1	0.1	7.7	11.3
	Southwest Bering Sea	July 1-5	0.60	50	100	57.9	0	0	0	10.0	10.0
		Average	0.60	50	100	57.9	0	0	0	10.0	10.0
Chum	Northwest Pacific Ocean	June 11-29	2.23	167	76	58.7	1.2	0	0	3.6	4.8
		July 8-18	2.92	102	68	58.7	2.9	1.0	0	4.9	8.8
		August 16-21	3.03	62	76	57.6	1.6	1.6	0	6.5	9.7
		September 12-14	0.70	16	100	55.6	25.0	12.5	0	6.3	43.8
		Average	2.2	347	80	57.7	7.7	3.8	0	5.3	16.8
	Southwest Bering Sea	July 1-5	2.60	54	87	58.9	0	1.9	0	3.7	5.6
		Average	2.60	54	87	58.9	0	1.9	0	3.7	5.6
Pink	Northwest Pacific Ocean	June 11-29	5.50	355	100	44.1	1.7	0	0	2.5	4.2
		July 8-18	3.33	129	100	47.1	0.8	2.3	0	9.3	12.4
		August 16-21	0.53	30	100	50.8	10.0	3.3	0	20.0	33.3
		Average	3.0	568	100	47.3	4.2	1.9	0	10.6	16.6
	Southwest Bering Sea	July 1-5	27.53	200	100	44.7	0	0.5	0	4.5	5.0
		Average	27.53	200	100	44.7	0	0.5	0	4.5	5.0
Chinook	Northwestern Pacific Ocean	June 11-29	0.01	25	61	69.6	4.0	0	0	12.0	16.0
		July 8-18	0.02	2	12	54.5	0	0	0	50.0	50.0
		August 16-21	0.08	-	-	-	-	-	-	-	-
		September 12-14	0.03	-	-	-	-	-	-	-	-
		Average	0.04	27	18	62.1	1.0	0	0	15.5	16.5
	Southwest Bering Sea	July 1-5	0.01	6	75	65.2	0	0	0	0	0
		Average	0.01	6	75	65.2	0	0	0	0	0
Coho	Northwest Pacific Ocean	July 8-18	0.43	42	100	58.4	4.8	0	0	9.5	14.3
		August 16-21	2.13	80	100	57.8	1.3	0	0	7.5	8.8
		September 12-14	1.20	28	100	57.3	7.1	0	0	10.7	17.8
		Average	0.9	156	100	57.8	4.4	0	0	9.2	13.6

from the nets in front of the fishing vessel. Fur seals often take only one bite instead of eating the entire fish, which greatly reduces the final quality of salmon in commercial catches. Moreover, the importance of fur seal predation on salmon in the northwest North Pacific Ocean and southwest Bering Sea can be confirmed indirectly by assessments showing their recent high level of abundance in the Commander Islands (up to 200,000 individuals; Kuzin 2003). We do not have any records of the occurrence of fur seals or other species of pinnipeds in our gillnets in 2004, although dead fur seals usually have not been observed in the nets. We cannot exclude other species of pinnipeds as potential consumers of salmon during drift gillnet fishing. For this reason, we clas-

sified all seal bites as Type II because accurate identification to species did not seem possible.

Other types of predators affecting salmon during drift gillnet fishing should also be considered. In general, seabirds (mostly fulmars and albatrosses) try to attack fish caught by gillnets, particularly fish caught near the upper rope of the gillnet. Usually, seabirds peck at salmon flesh in several different places, which further reduces the commercial value of the catch. This feeding behavior often leads to seabird mortality, if the birds become entangled in the nets.

Cetacean species are another potential cause of wounds on salmon. The most frequent cetacean in salmon gillnet by-catch is Dall's porpoise (*Phocoenoides dalli*). Unfortunate-

Table 3. The incidence (% of N) of immature Pacific salmon in gillnet catches with wounds caused by some species of predators. N = number of fish.

Species	Region	Period in 2004	CPUE (fish/tan)	N	Immature in catch (%)	Length (cm)	Type I (fish) a	Type I (fish) b	Type I (fish) c	Type II (seal)	Total incidence (%)
Sockeye	Northwest Pacific Ocean	June 11-29	1.44	10	5	49.9	0	0	0	0	0
		July 8-18	4.88	101	50	48.5	0	0	0	4.0	4.0
		August 16-21	2.47	73	79	49.3	2.7	1.4	0	2.7	6.8
		September 12-14	6.50	156	100	48.9	2.6	1.3	0	1.9	5.8
		Average	3.8	340	58	49.2	1.3	0.7	0	2.2	4.2
	Southwest Bering Sea	July 1-5	0.60	-	-	-	-	-	-	-	-
		Average	0.60	-	-	-	-	-	-	-	-
Chum	Northwest Pacific Ocean	June 11-29	2.23	53	24	53.6	0	0	0	0	0
		July 8-18	2.92	47	32	50.7	2.1	0	0	8.5	10.6
		August 16-21	3.03	20	24	51.1	5.0	0	0	0	5.0
		September 12-14	0.70	-	-	-	-	-	-	-	-
		Average	2.2	120	20	51.8	1.8	0	0	2.1	3.9
	Southwest Bering Sea	July 1-5	2.60	8	13	53.4	0	0	0	0	0
		Average	2.60	8	13	53.4	0	0	0	0	0
Chinook	Northwest Pacific Ocean	June 11-29	0.01	16	39	70.5	0	6.3	0	0	6.3
		July 8-18	0.02	15	88	66.9	0	0	0	0	0
		August 16-21	0.08	23	100	66.0	0	0	0	8.7	8.7
		September 12-14	0.03	21	100	61.3	9.5	0	0	4.8	13.3
		Average	0.0	75	82	66.2	2.4	1.6	0	3.4	7.1
	Southwest Bering Sea	July 1-5	0.01	2	25	69.5	0	0	0	0	0
		Average	0.01	2	25	69.5	0	0	0	0	0

ly, we did not have enough data to identify wounds caused by cetaceans. Nevertheless, attempts to assess this problem have already been undertaken by other researchers. According to observations by Kaplanova and Zolotukhin (2002), the Amur River salmon have wounds identified as the bites of white whales (*Delphinapterus leucas*). However, we did not observe such bites during our study. Recently, the first information was received from fishermen about killer whale (*Orcinus orca*) attacks on salmon in gillnets near the northern Kuril Islands. This problem is currently becoming serious enough to create a threat to the commercial longline fishery for halibut and cod in the Sea of Okhotsk.

During the cruise of the R/V *Ecopacific* in 2004, there were no recorded cases of fish with secondary net marks. We expected to see secondary net marks because gillnet fishing occurs in open waters of the North Pacific Ocean and the Bering Sea during the initial stages of commercial fisheries along salmon migration routes. The problem of secondary net marks is characteristic of offshore and river fisheries.

We also recorded the condition of wounds as "fresh" and "healed". These data are not provided in this document, because 80–90% of all wounds observed during the cruise were obviously "fresh." In addition, fresh and healed wounds do not provide insight into losses caused by predators. Many

of the fresh wounds on salmon in gillnets are a direct consequence of increased availability of net-caught fish to predators. Wounding among fish in gillnet catches is several times higher than that in nature, e.g., as in the case of fur seal activity. Thus, if a wound occurred shortly before the fish was caught in a driftnet, the wound was considered "natural" and "fresh." A major problem in the analysis of wounded salmon caught in gillnets is that the differentiation of wounds into "natural" and "not natural" is never absolute.

We emphasize that the results of our analysis are only an indicator of the possible influence of predators on the abundance of salmon. In essence, our results can be interpreted as background monitoring helpful to analysis of the situation as a whole. Perhaps data from trawl catches may be more informative than gillnet data, because the time of predator-prey contact in trawl gear is limited. Moreover, investigations of wounded salmon caught in trawl gear have already been undertaken (Sviridov et al. 2004). At present, all that is needed to advance to the applied stage is the standardization of methods and organization of field data records.

Northwest North Pacific Ocean
Most of our observations were made in the northwest North Pacific Ocean (Tables 2 and 3). The large volume
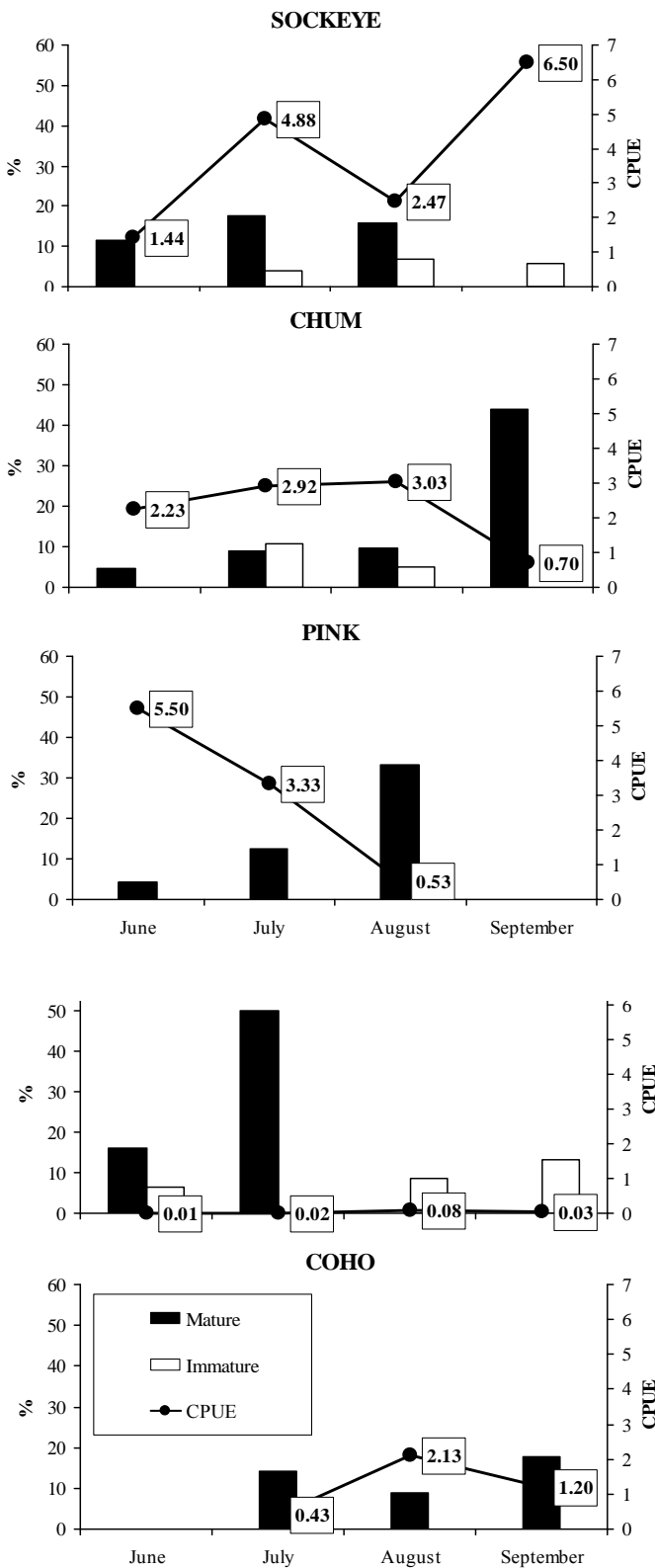
Fig. 3. Temporal (monthly) dynamics of the relative abundance of Pacific salmon (catch per unit effort (CPUE, fish/net) and percentages of mature and immature salmon with wounds caused by piscivorous fishes and seals in the northwest North Pacific Ocean in June-September 2004.

of data from this region allows us to gain insight into the temporal (monthly) dynamics of wounded salmon in gillnet catches (Fig. 3).

Sockeye Salmon: In June–September sockeye salmon were the most abundant species in gillnet catches in the northwest North Pacific Ocean (1.44–6.50 fish/net). The total percentage of mature sockeye salmon with wounds averaged 11.3% (range 11.6–17.6%). The highest numbers of fish with wounds were observed in July and August. Most wounds were identified as Type II (seals); average 7.7%; range 7.4–12.7%). The maximum number of both types of wounds occurred in July. The next most frequent wounds were Type I–a (longnose lancetfish or North Pacific daggertooth; average 3.4%; range 3.2–5.3%; peak in August). The percentage of sockeye salmon with wounds caused by lampreys (Type I–b) was low (average 0.1%). Only one wound identified as a salmon shark bite was recorded in June (Type I–c). The total percentage of wounding in immature sockeye salmon was lower than that of mature fish (average of 4.2%; range 0–6.8%; peak in July). Wounds caused by seals were the most frequent (average 2.2%, range 0–4.0%), followed by longnose lancetfish and North Pacific daggertooth wounds (average 1.3%; range 0–2.7%). The percentage of immature fish with lamprey wounds was somewhat higher than that of mature fish (average 0.7%; range 0–1.4%).

Chum Salmon: Chum salmon were also relatively abundant in the catches in this area (0.70–3.03 fish/net). Wounding of mature chum salmon in this area was extremely variable (average 16.6%; range 4.8–43.8%; peak in September). The most frequent wounds were caused by longnose lancetfish and North Pacific daggertooth (average 7.7%; range 1.2–25.0%; peak in September). The percentage of chum salmon with wounds caused by seals averaged 5.3% (3.6–6.5%), and there was no clear temporal trend in incidence. The percentage of chum salmon with lamprey wounds was relatively high compared to other salmon species (average 3.8%; range 0–12.5%; peak in August). The total percentage of wounding in immature chum salmon was lower than in mature fish (average 3.9%; range 0–10.6%). The wounds were mostly caused by pinnipeds (average 2.1%; range 0–8.5%) and longnose lancetfish and North Pacific daggertooth (average 1.8%; range 0–5.0%). No other types of wounds were observed.

Pink Salmon: Pink salmon catches in this area varied between 0.53–5.50 fish/net. All pink salmon in the gillnet catches were mature. The percentage of pink salmon with wounds in June–August averaged 16.6% (range 4.2–33.3%). The peak was recorded in August, i.e., at the very end of the prespawning run. The highest percent of wounds were caused by seals (average 10.6%; range 2.5–20.0%). The percentage of salmon with wounds caused by piscivorous fishes was somewhat lower than those caused by seals (longnose lancetfish and North Pacific daggertooth: average 4.2%, range 1.7–10.0%; lamprey: average 1.9%; range 0–3.3%).

Chinook Salmon: The relative abundance of chinook
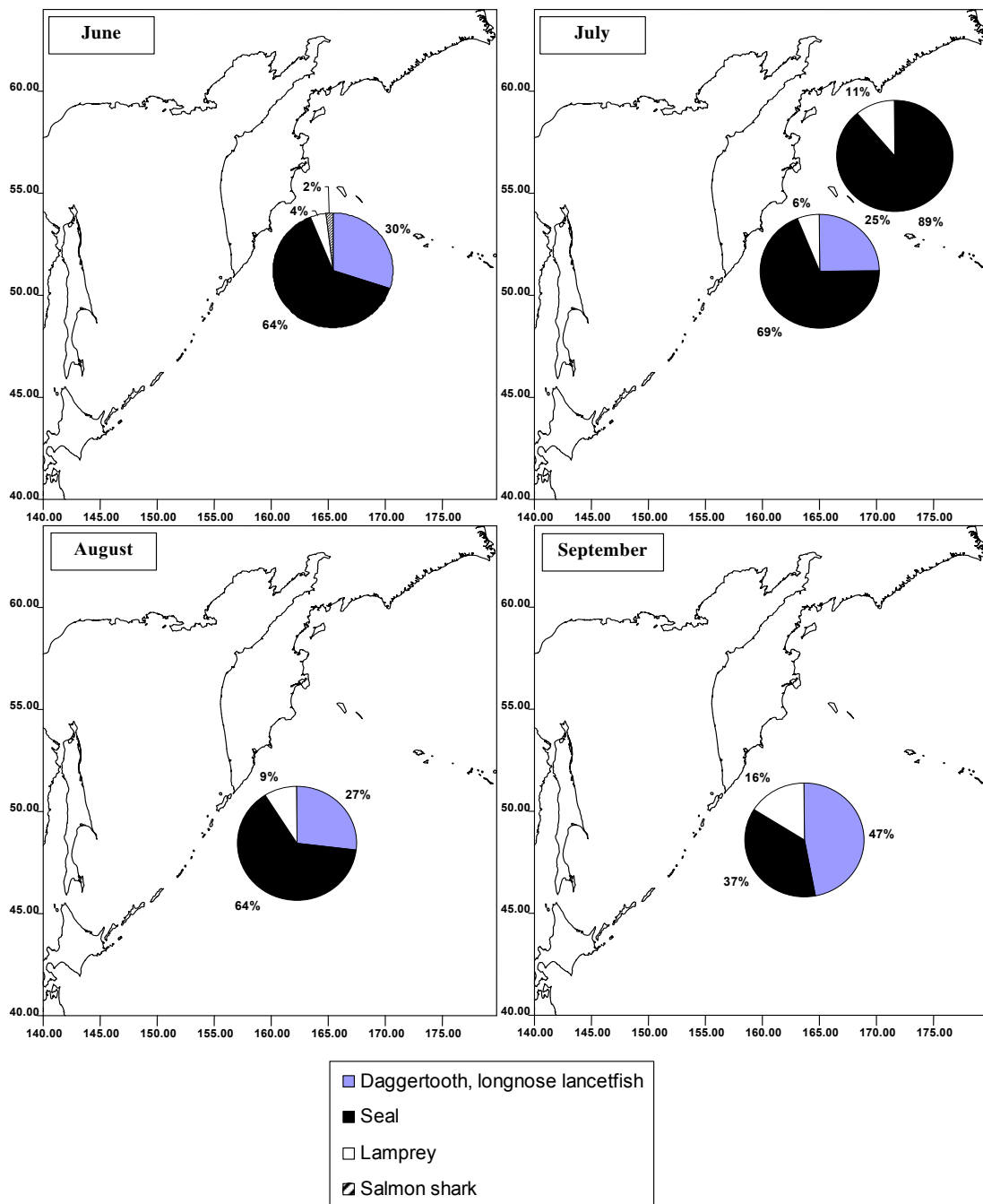
Fig. 4. Distribution (%) of wounds caused by four types of predators on all species of mature and immature Pacific salmon caught by drift gillnets in June-September 2004 in the northwest North Pacific Ocean and southwest Bering Sea.

salmon was low throughout the period of observation (range 0.01–0.08 fish/net). The percentage of mature chinook salmon with wounds in the northwest North Pacific Ocean in June–July averaged 16.5% (range 16.0–50.0%). The wounds were mostly Type II (seals; average 15.5%; range 12.0–50.0%). Longnose lancetfish and North Pacific daggertooth attacked mature chinook salmon less frequently than the other salmon species (average 1.0%; range 0–4.0%). The total percentage

of wounding of immature chinook salmon was lower than that in mature chinook (average 7.1%; range 0–13.3%). The percent of immature chinook salmon with wounds caused by seals (average 3.4%; range 0–8.7%) and fishes (average 2.4% by longnose lancetfish and North Pacific daggertooth, and 1.6% by lampreys) were similar.

Coho salmon: Over the entire period of observations, the CPUE of coho salmon varied from 0.43 to 2.13 fish/net.

All coho salmon in the gillnet catches were mature. The percent of coho salmon with wounds averaged 13.6% (8.8–17.8%). The percent of coho salmon with wounds caused by seals averaged 9.2% (7.5–10.7%). The percent of coho salmon with wounds caused by longnose lancetfish and North Pacific daggertooth averaged 4.4% (range 1.3–7.1%).

Southwestern Bering Sea

Because observations in the southwestern Bering Sea were limited to early July, we do not have information on monthly variation in the incidence of salmon wounded by predators in this region. Nevertheless, the data for the major species of Pacific salmon caught by gillnets in early July are informative (see Tables 2 and 3).

Sockeye Salmon: The incidence of predation on mature sockeye salmon in this area was higher than that of other Pacific salmon species. Approximately 10.0% of the sockeye salmon had wounds, and all the wounds were identified as seal bites. Immature sockeye salmon were not observed during this period.

Chum Salmon: A total of 5.6% mature chum salmon in the southwestern Bering Sea had wounds (3.7% caused by seals, and 1.9% by lampreys). There were no wounds observed on immature chum salmon.

Pink Salmon: Pink salmon were the most abundant species of salmon in the southwestern Bering Sea in early July, and as a result the sample size of pink salmon is the most representative. A total of 5.7% of the pink salmon had wounds (4.5% caused by pinnipeds, and 0.5% by lampreys).

General Trends in the Incidence of Predation in Gillnet Catches

We pooled our data on predator marks over all mature and immature Pacific salmon species to illustrate some general trends the distribution of wounds by four types of predators in the northwest North Pacific Ocean and southwestern Bering Sea in the summer–autumn period (Fig. 4). The results clearly show that in June–August, i.e., the principal period of prespawning salmon migrations, most wounds were caused by seals (64–69% of wounds observed on salmon in North Pacific waters adjacent to Kamchatka; 89% in the southwestern Bering Sea). In September in catches from the southeast coast of Kamchatka and northern Kuril Islands, the percentage of seal wounds decreased to 37%. Wounds caused by longnose lancetfish and North Pacific daggertooth were observed only in the northwest North Pacific Ocean. However, our observation period in the southwest Bering Sea was not long enough to make any firm conclusions about regional differences in wounds caused by longnose lancetfish and North Pacific daggertooth. During summer, 25–37% of wounds were caused by longnose lancetfish and North Pacific daggertooth, and the highest percentage (47%) of wounds by these species was observed in September. Lamprey wounds demonstrated the most spatial and tempo-

ral variability (4–16% of wounds in the northwest North Pacific Ocean; up to 11% in the southwestern Bering Sea). The percentage of wounds caused by salmon sharks was very low in our study, which is probably because most salmon die from shark attacks. The only case of a salmon shark bite was recorded in June in the North Pacific waters adjacent to Kamchatka.

Three general trends in our results can be suggested. These mostly concern mature salmon, because our study exactly overlapped the period of their prespawning migrations. First, the incidence of wounds does not depend on the body size of salmon. For example pink salmon, which is the smallest Pacific salmon species, had an incidence of wounds similar to that of chinook salmon, which is the largest Pacific salmon species. We also did not find any intraspecific size-dependent effects. Second, most wounding of salmon in gillnet catches is caused by seals, longnose lancetfish, and North Pacific daggertooth. There was no prey-selectivity preference observed among predators. We cannot exclude the possibility that the observed incidence of wounds is overestimated, because salmon in gillnets are readily available prey. This especially concerns the incidence of wounds by seals. Third, the percentage of regenerated wounds (scars) in mature salmon increased at the end of the prespawning run. Although timing varied by species, the percent of salmon with visable scars increased during the migration (below 10–20% in early and mid periods, and up to 40–50% in the late period). This trend may be directly related to salmon physiology, i.e., the energy expended to regenerate injured tissues may delay maturation.

CONCLUSION

The data presented here include our observations of wounds among Pacific salmon during a gillnet survey in the Exclusive Economic Zone of the Russian Federation in summer–autumn 2004. We present a method to classify field observations of wounds into the types caused most frequently by different predators during prespawning migrations of salmon in the open ocean. The incidence of wounds was assessed by species of predator. Some general trends typical for all Pacific salmon species were revealed. First, the incidence of wounds does not depend on salmon body size at either the intra- or inter-specific level. Second, wounds on salmon in gillnet catches were caused most frequently by seals (37–69% of wounds on salmon in North Pacific waters adjacent to Kamchatka; 89% of wounds in the southwest Bering Sea) and two piscivorous species of fish, longnose lancetfish and North Pacific daggertooth (25–47% of wounds in North Pacific waters adjacent to Kamchatka). The percentage of lamprey wounds was lower (4–16% of wounds in North Pacific waters adjacent to Kamchatka; 11% in the southwest Bering Sea). Third, the percentage of regenerated wounds (scars) in mature salmon increased at the end of the prespawning migration. We plan to continue to classify wounds on salmon

by predator type during future gillnet surveys in the Russian Economic Zone.

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Preliminary Studies of Metazoan Parasites of Chum Salmon (*Oncorhynchus keta*) in Korea

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Abstract: The parasites of chum salmon (*Oncorhynchus keta*) in Korea have not been described. We investigated metazoan parasites of 80 adult chum salmon caught in 2004 in the Namdae River, Korea. Parasite species found were 1 digenea (unidentified), 3 cestodes (*Eubothrium* sp., *Nybelinia* sp. plerocercoid, 1 unidentified), 3 nematodes (*Anisakis simplex* larva, *Contracaecum* sp. larva. *Hysterothylacium* sp. larva), and 1 copepod (*Lepeophtheirus salmonis*). All fish examined had at least 1 parasite species. The most abundant parasite was *Eubothrium* sp. (93.8% of fish examined were infected), and the number of *Eubothrium* sp. from infected fish ranged from 29 to > 100 per individual fish. An unidentified digenean species was recorded in 25 fish. Similarly, the precise identification of some nematode species was not possible. The prevalence of infection by *L. salmonis* was low (6%). More detailed and larger-scale studies should be conducted in order to provide important and precise information on the parasitic fauna of chum salmon in Korean waters.

Keywords: *Oncorhynchus keta*, adult chum salmon, metazoan parasites, Korea

INTRODUCTION

By investigating parasitic fauna of fish species, much information for studying population structure, stock identification, migration routes, and diet can be obtained. Although there are limitations on using parasites as biological tags for population studies of marine fishes (see Arthur 1997), there are also advantages over other tagging methods. In particular, such techniques are less expensive and more appropriate for investigating small delicate fish and invertebrates (MacKenzie and Abaunza 1998).

Knowing the geographical origin of salmonid fishes caught in the North Pacific is helpful in developing fish stock management programs. Since Margolis (1963) published the first report on the oceanic distribution of western Alaskan and Kamchatkan sockeye salmon (*Oncorhynchus nerka*) by using parasites as biological tags, many researchers have applied this technique to clarify the geographical distribution and stock identification of salmonid fishes (see a review by Urawa 1989).

Korea has active salmon enhancement operations and fisheries. Most of the catch consists of chum salmon (*O. keta*). To date, no systematic efforts have been made to investigate either migration routes or migration rates.

The present study was undertaken to identify metazoan parasites of chum salmon in Korean waters and to examine the potential use of these metazoan parasites for studying salmon biology.

MATERIALS AND METHODS

We investigated metazoan parasites of 80 adult chum salmon (fork length 56.2–70.5 cm; body weight 2.35–6.67 kg) returning to the Namdae River along the northeast coast of Korea in October and November of 2004. They were captured by a river-blocking set net at the mouth of the river. Whole fish were frozen and transported to the laboratory, where they were measured, thawed and examined for metazoan parasites. External parasites were fixed in either 10% buffered formalin or 70% ethanol, and identified. Gastrointestinal tracts were opened longitudinally, and the contents rinsed into beakers and examined for endoparasites. These parasites were fixed in ammonium picrate-glycerin or 10% buffered formalin, and stained when necessary. All parasites found were identified to the lowest taxon possible, and the prevalence of infection (percentage of hosts infected with a particular parasite) was determined. Intensity is the number of a particular parasite species in an individual infected host.

Table 1. Prevalence of infection (%) and mean intensity (± S.D.) of metazoan parasites from adult chum salmon (n = 80) in the Namdae River, Korea.

	Prevalence of infection (%)	Mean Intensity	Infection Site
Unidentified Digenea sp.	31.3%	6.08 ± 3.74	Gastrointestinal tract
Eubothrium sp.	93.8%	71.2 ± 23.9	Intestine
Nybelinia sp. plerocercoid	28.8%	2.82 ± 1.99	Musculature
Unidentified Cestoda sp.	NC[1]	NC	Intestine
Anisakis simplex larva	17.5%	1.36 ± 0.63	Body cavity, musculature
Contracaecum sp. larva	8.8%	1.13 ± 0.35	Body cavity, musculature
Hysterothylacium sp. larvae	5.0%	1.25 ± 0.50	Body cavity, musculature
Unidentified Nematoda sp.	NC	NC	Body cavity
Lepeophtheirus salmonis	6.3%	2.40 ± 1.14	Skin, fin

[1]NC, Not counted.

RESULTS

Parasite species found were 1 digenea (unidentified), 3 cestodes (*Eubothrium* sp., *Nybelinia* sp. plerocercoid, 1 unidentified), 3 nematodes (*Anisakis simplex* larva, *Contracaecum* sp. larva, *Hysterothylacium* sp. larva), and 1 copepod (*Lepeophtheirus salmonis*) (Table 1). All fish examined had at least 1 parasite species. The most abundant parasite was *Eubothrium* sp. (93.8% of fish examined were infected), and the number of *Eubothrium* sp. from infected fish ranged from 29 to > 100 per individual fish. Due to difficulties in the identification of intestinal cestodes, the data recorded may possibly be changed by further investigation. An unidentified digenean species was recorded in 25 individual fish. Similarly, the identification of some nematode species was not possible. The unidentified digeneans, cestodes and nematodes await further identification. Sea lice (*L. salmonis*) were recorded from the skin of fish and despite the low prevalence with a mean intensity of 2.4 (Table 1).

DISCUSSION

More than 60 species of parasites have been used as biological tags for studying salmon biology (see Urawa 1989). The ocean distribution determined by parasite studies of Pacific salmon has been frequently studied (see review by Margolis 1992). However, studies of the parasitic fauna of chum salmon are uncommon.

We found 9 species of parasites from adult chum salmon in this study. Most of them are parasites frequently found in Pacific salmon. The prevalence of infection of *Anisakis simplex* larvae was unexpectedly low, compared with the prevalence of this parasite in chum salmon in Japan (Urawa and Fujisaki 2006). There is no clear explanation for the low prevalence at the present time. However, the insufficient ef-

fort in investigating nematodes, especially in musculature, may be one possible reason.

In this study, chum salmon were collected from only one location so direct comparisons with other stocks were not possible. More detailed and larger-scale studies, involving the precise identification of parasites found and comparing them with those of other stocks, are necessary for providing useful information on chum salmon populations in Korea. Myxosporean parasites have been used successfully as biological tags in salmonid fishes (Awakura et al. 1995; Urawa et al. 1998), and should be included in future surveys of parasites of chum salmon in Korea.

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Stock-Specific Distributions of Asian and North American Salmon in the Open Ocean, Interannual Changes, and Oceanographic Conditions

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Abstract: Knowledge of migration routes, migration timing, and resident areas for populations of Pacific salmon in the open ocean is vital to understanding their status and role in North Pacific marine ecosystems. In this paper we review information from the literature, as well as some previously unpublished data, on stock-specific distribution and migration patterns of salmon in the open ocean, interannual variation in these patterns, and associated ocean conditions, and we consider what this information can tell us about ocean conditions on small- to mid-size scales. We conclude that climate-driven changes in open-ocean feeding areas and along the migratory routes of Asian and North American salmon can result in predictable interannual changes in stock-specific distribution, migration patterns, and other biological characteristics. Global climate change is currently causing more frequent and un-predictable environmental changes in the open ocean habitats through which salmon migrate. Data on changes in the distribution and migration of indicator stocks of adult salmon returning from the open ocean might provide an "advance warning" of interannual changes in North Pacific marine ecosystems.

Keywords: salmon, ocean, distribution, stocks, interannual variation, oceanographic conditions

INTRODUCTION

For more than fifty years, research studies coordinated by the International North Pacific Fisheries Commission (INPFC 1955–1992) and the North Pacific Anadromous Fish Commission (NPAFC 1993-present) have focused on determining distribution and migration patterns of Pacific salmon (*Oncorhynchus* spp.) in the open ocean (e.g., see data syntheses and reviews by Godfrey et al. 1975; French et al. 1976; Neave et al. 1976; Major et al. 1978; Takagi et al. 1981; Burgner 1991; Healey 1991; Heard 1991; Salo 1991; Sandercock 1991). This large body of work has led to some general hypotheses about oceanic distribution and migration of salmon populations, and in particular about: (1) migration routes, migration timing, and resident areas of Pacific salmon as population- or stock-specific traits, and (2) variation in ocean conditions (e.g., temperature, salinity, ocean currents) that can influence stock-specific distribution and migration patterns. Scientists have long recognized, however, that re-

lations among salmon distribution, migration patterns, and environmental conditions in the open ocean are obscured when stocks from different continents, geographic regions, and sub-regions intermix (e.g., Manzer et al. 1965; Takagi et al. 1981). Until recently, significant progress in research on this issue has been limited by the lack of comprehensive baseline data on salmon populations throughout the Pacific Rim and of accurate methods for identifying salmon stocks migrating through the open ocean (e.g., NPAFC 2004).

In a recent review and synthesis of information on salmon behavior and ecology, Quinn (2005) concluded that "we still have little direct information on the movement patterns and orientation mechanisms used by salmon on the open ocean." While it is beyond the scope of our paper to resolve these major questions, we hope to draw attention to these issues as a focus for future research on the status and role of Pacific salmon in North Pacific marine ecosystems.

Our specific objectives in this paper are as follows: (1) provide a brief overview of information on stock-specific

distribution and migration patterns of salmon on different spatial and temporal scales in the open ocean, (2) provide examples of interannual variation in salmon distribution and migration in relation to ocean conditions, (3) review some recent changes in ocean conditions (physical) that may affect stock-specific salmon distribution and migration patterns, and (4) consider whether annual variation in stock-specific distribution and migration patterns can tell us something about changes in ocean conditions.

MATERIALS AND METHODS

This paper synthesizes previously published scientific literature and processed research reports, and analyzes both published and unpublished data. Over the years, many different materials and methods have been used to sample and analyze salmon and surrounding oceanic conditions. Samples were not collected consistently by location, time, or intensity. Capture methods included purse seines, longlines, gill nets, and surface trawls (e.g., Hartt 1975; Karpenko et al. 2005). Stock identification techniques have included high seas tagging, serology, morphometry, scales (measuring age, circuli patterns, or both), natural parasite tags, genetic analysis (allozyme and DNA), otolith marks, and coded-wire tags (e.g., Hartt 1962; Myers et al. 2004). Oceanographic observations were made independently (e.g., Favorite et al. 1976), directly aboard chartered fishing vessels at fishing stations, (e.g., Eisner et al. 2005), or jointly in fisheries-oceanographic surveys aboard research vessels (e.g., Khen and Basyuk 2005).

Because of limited space, we do not attempt a comprehensive review, and instead we focus on research pertaining to a few major premises. These premises include: (1) Pacific salmon in the open ocean have stock-specific distribution and migration patterns, (2) interannual variation in salmon distribution in the open ocean during the spring-summer season depends largely on ocean conditions during the preceding winter, (3) circulation and climate systems in the North Pacific Ocean and Bering Sea are interconnected, and (4) oceanographic conditions in these regions have been changing significantly over the past several decades, even prior to the climatic regime shift of 1977.

We use the term "juvenile" to denote salmon in their first ocean year, and "immature" or "maturing" to indicate older fish. By our definition, the "open ocean" refers primarily to deep-water oceanic regions beyond neritic waters (< 200 m deep) over the continental shelf. The majority of our samples were maturing pink salmon (*O. gorbuscha*) and immature and maturing chum (*O. keta*) and sockeye (*O. nerka*) salmon, which are the most abundant maturity groups and, more generally, Pacific salmon species inhabiting the open ocean. The data from high-seas, salmon-tagging experiments used in a few examples are from a shared NPAFC database that is currently updated and archived by the High Seas Salmon Research Program, School of Aquatic and Fishery Sciences, University of Washington, Seattle.

RESULTS AND DISCUSSION

Stock-specific Distribution and Migration Patterns of Salmon in the Open Ocean

A major premise of this review is that Pacific salmon in the open ocean have stock-specific distribution and migration patterns. This is not a new idea. Moiseev (1956) was one of the first scientists to publish evidence that the marine habitats of individual stocks of salmon are located in specific areas of the open ocean. Recent genetic work in freshwater habitats has revealed a strongly hierarchical structuring of genetic variation that descends by geography from the largest scale (i.e., ancestral) geographic lineages, to regional geographic subdivisions, to individual subbasins, and to life-history subdivisions within these subbasins (Utter et al. 1989; see review by Williams et al. 2006). We hypothesized that the distribution patterns of salmon populations in the open ocean would also have a hierarchical geographic structure, i.e., stocks that are genetically similar or geographically adjacent to each other in freshwater habitats, or both, have ocean distribution and migration patterns that are more similar to each other than those of populations that are genetically or geographically distant. Individual populations or life-history variants within populations usually occupy only a portion of the entire oceanic range occupied by larger groups of populations, e.g., regional stock complexes.

On the largest spatial scale, Pacific salmon species migrating in open waters of the North Pacific Ocean are distributed primarily in the region north of the sub-arctic boundary (Fig. 1). Pearcy (1992) speculated that the evolutionary "divergence of North Pacific salmonids and their emergence as successful and abundant fishes is related to the formation of the cold Subarctic Water Mass in the North Pacific." Across this immense marine region, the known ranges of salmon encompass most major oceanic currents and domains (Fig. 1). Marine habitat conditions (e.g., sea temperatures and salinities) within acceptable limits for salmon, however, can sometimes extend south of the sub-arctic boundary, which expands the salmon's known open ocean range into subtropical waters (Azumaya et al. 2007).

Early models of open-ocean migration patterns from INPFC-coordinated research described salmon movements at sea as counterclockwise circles, generally "downstream" in cyclonic gyres and through associated currents in the western North Pacific, Gulf of Alaska, and Bering Sea (Royce et al. 1968). Although this outdated model is still frequently cited in the recent scientific literature, the prevailing theory among experts is that salmon in the open ocean move across broad fronts—to the south and east in winter and spring and to the north and west in summer and fall (e.g., French et al. 1976; Burgner 1991; Shuntov et al. 1993). These broad seasonal shifts in distribution likely reflect both genetic adaptations and behavioral responses to environmental cues (e.g., prey availability and water temperature) that are mediated by
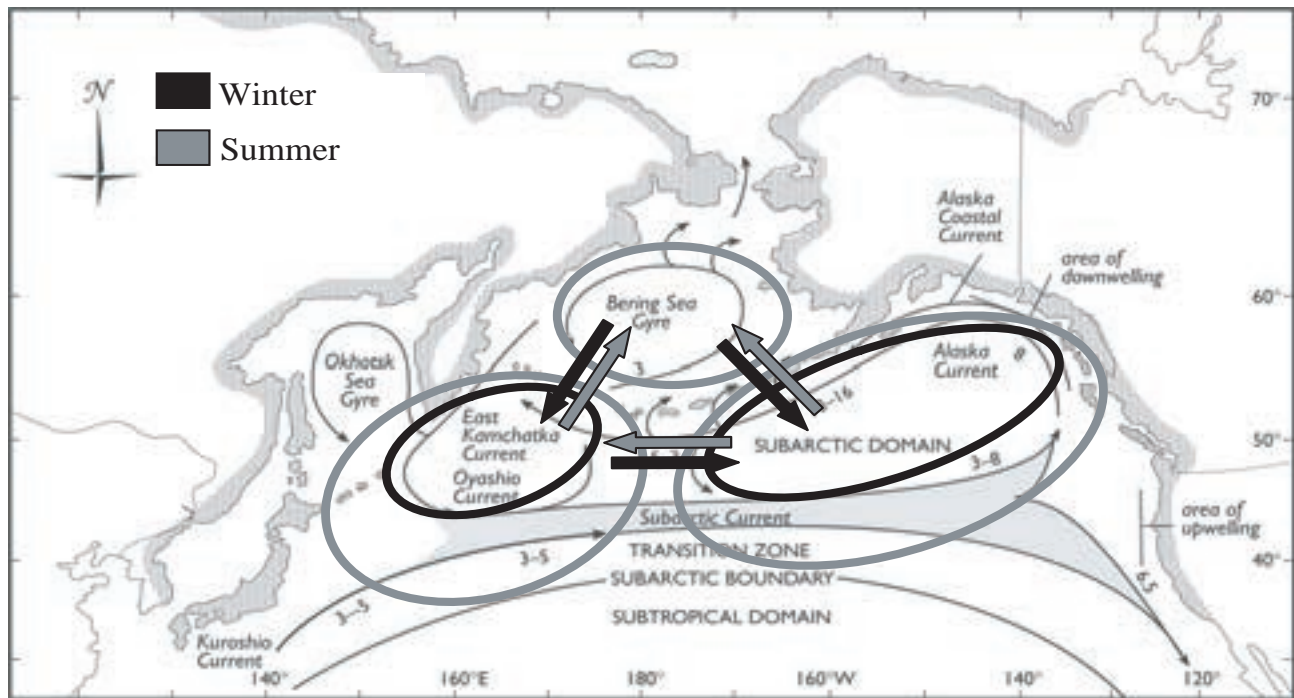
Fig. 1. A general conceptual model of seasonal distribution and movements of Pacific salmon in the open ocean. Salmon are distributed in both the Bering Sea and North Pacific Ocean in the summer and primarily in the North Pacific Ocean in the winter. Immature salmon generally move to the south and east in winter (black arrows) and to the north and west in summer (grey arrows). Base map showing oceanographic features and approximate current speed (km/d) is from Quinn (2005).

bioenergetic constraints.

A general seasonal model of the open ocean distribution of immature and maturing Pacific salmon indicates that in winter and spring they are primarily distributed south of the Commander Island-Aleutian Island chain in the North Pacific Ocean, and in summer and fall they are widely distributed throughout the North Pacific Ocean and Bering Sea (Fig. 1). However, there are major exceptions to this general model. For example, the Bering Sea is a major winter habitat for Asian and North American populations of Chinook salmon (*O. tshawytscha*) (Radchenko and Glebov 1998; Myers and Rogers 1988).

During their first year in the ocean, juvenile Asian and North American salmon intermingle rarely. Although data are limited, most juvenile pink, chum, and sockeye salmon move in late fall or early winter from relatively shallow, coastal waters to surface waters over the deep ocean basins (e.g., Hartt and Dell 1986; see recent national reviews of the early marine period in Myers et al. 2000 and NPAFC 2003). Possible exceptions are Russian and western Alaskan stocks of juvenile salmon, which may intermingle during their first summer and fall in the northeastern Bering Sea (Farley et al. 2005).

At the scale of major geographical lineages or continent-of-origin and regional stock complexes, open ocean distributions of immature and maturing Asian and North American salmon are frequently depicted by composites of recovery data from INPFC/NPAFC-coordinated high seas salmon tagging experiments (e.g., French et al. 1975; Myers et al. 1990, 1996; Klovach et al. 2002; Beamish et al. 2005). These data indicate that Asian stocks are primarily distributed west of 180°, while North American stocks are primarily distributed east of 180° (Fig. 2). The apparent areas of mixing between immature and maturing Asian and North American salmon in the open ocean vary by species, and are largest for chum salmon (174°E–140°W, 44°N–61°N), smaller for pink salmon (between 175°E and 160°W, 44°N–57°N), and smallest for sockeye salmon (165°E–175°W, 45°N–58°N) (Fig. 2). Differences between species in areas of mixing seem to be positively correlated with their relative abundance in the open ocean. For example, chum salmon are more abundant in the ocean than pink salmon, inhabit the ocean for more time (as many as five winters compared to one winter for pink salmon), and have a larger area of mixing.

Differences in the east-west extent of distribution also seem to be positively correlated with the relative abundance of Asian and North American salmon. For example, Asian pink and chum salmon are more abundant and have a more extensive east-west range than do North American pink and chum salmon (Fig. 2). Similarly, North American sockeye salmon are more abundant and have a more extensive east-west range than do Asian sockeye salmon (Fig. 2).

Asymmetrical distributions of Asian and North American salmon in the open ocean might reflect density-depen-
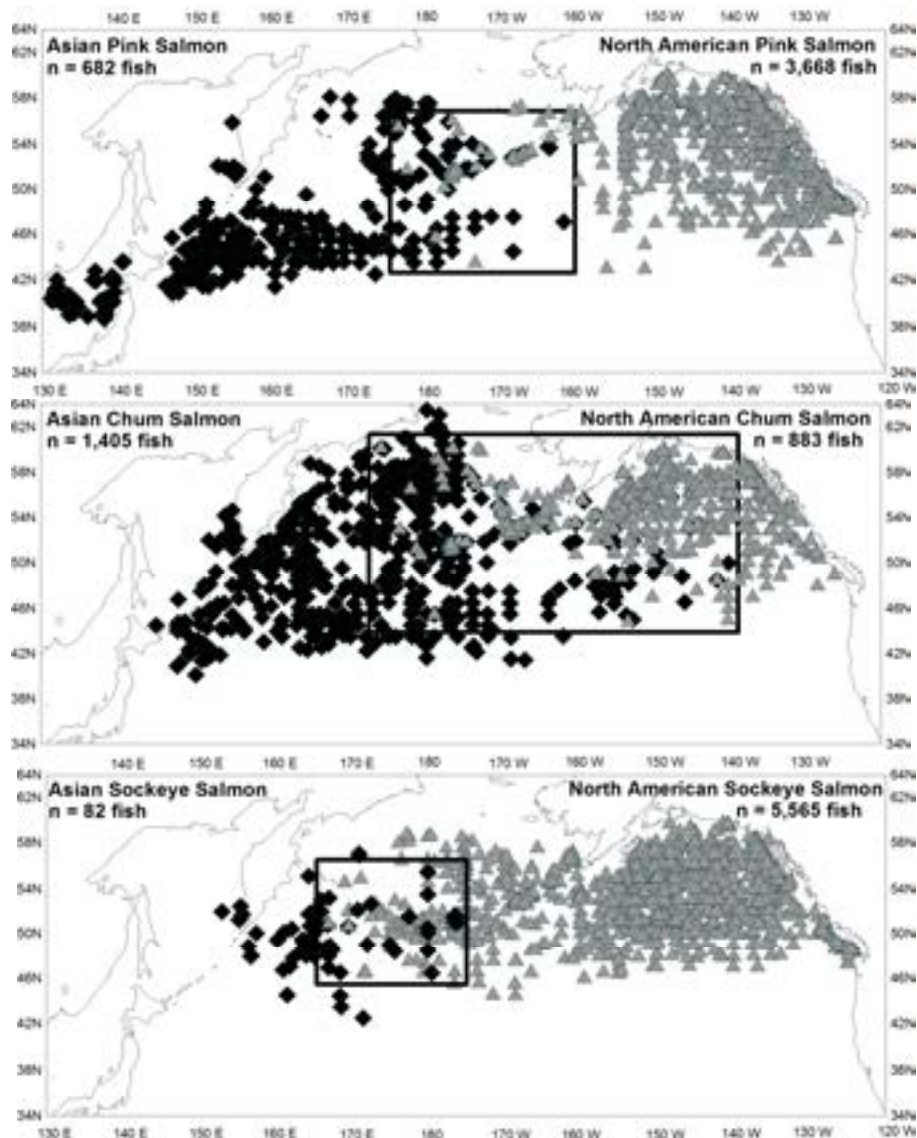
Fig. 2. Composite map showing overlap in open ocean distributions of Asian and North American salmon as observed in high-seas tagging experiments (1956–2004). Closed (black) diamonds = Asian stocks; closed (grey) triangles = North American stocks; open box = region of overlap. Data source: High Seas Salmon Research Program, University of Washington, Seattle.

dent interactions, as explained by the theory of "ideal free distribution" (Fretwell and Lucas 1970). That is, as competitive interactions increase in growing salmon populations, the population's geographic distribution increases until it reaches a new equilibrium. Ogura and Ito (1994) suggested that large-scale releases of hatchery chum salmon in Japan resulted in an expansion to their known oceanic range. However, detecting stocks at the limits of their geographic range might simply be easier when they are abundant. Asymmetrical distributions of Asian and North American salmon in the open ocean have also been attributed to physical oceanic factors, such as cold winter sea temperatures in the western North Pacific (e.g., Shepard et al. 1968; Neave et al. 1976) or passive (eastward) transport of immature Asian fish by wind-driven and geostrophic currents (Ueno et al. 1999; Azumaya

and Ishida 2004).

In the late 1970s, composite conceptual models of the distribution and migration routes of major regional stock complexes of Asian and North American salmon were developed by INPFC researchers using information from high-seas research and commercial fishing catch and effort data, biological data, tag recovery data, and stock-identification results (primarily natural parasite tags and analysis of scale patterns, e.g., French et al. 1976; Takagi et al. 1981). Burgner (1991) updated the French et al. (1976) sockeye salmon migration models with the results of scale pattern analyses conducted in the 1980s in the open ocean region south of 46°N (Harris 1987; see review by Myers et al. 1993). These conceptual models were a major breakthrough in our understanding of stock-specific migratory behavior of salmon
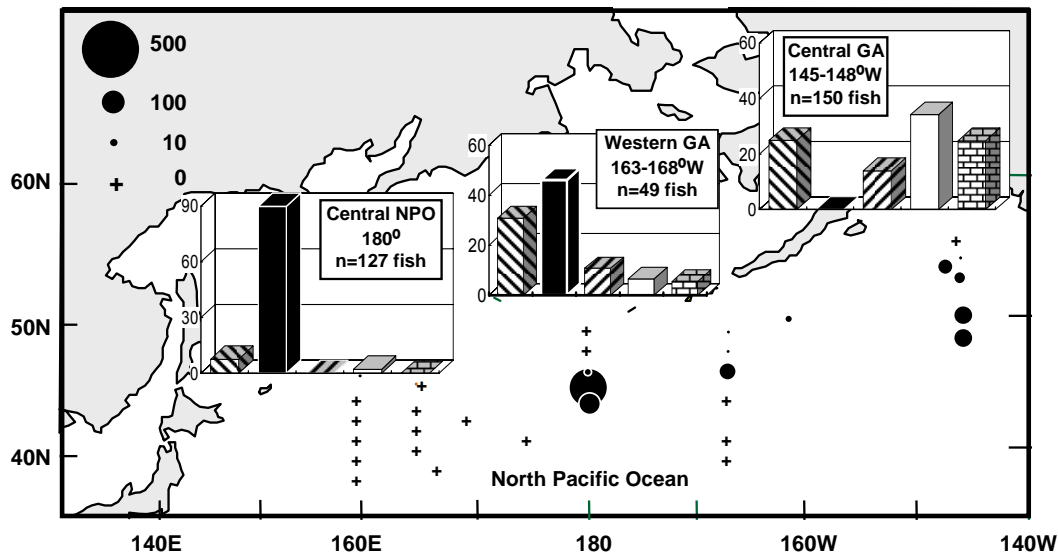
Fig. 3. Example of geographic variation in the regional stock composition of immature and maturing chum salmon in their 2nd-4th winters at sea, using a comprehensive baseline for 20 allozyme loci from stocks throughout the Pacific Rim (Urawa and Ueno 1997, 1999; Urawa 2000). Samples were collected during NPAFC-coordinated cooperative winter surveys of salmon aboard the Japanese research vessel *Kaiyo maru* in January 1996 and February 1998. The relative sizes of the solid circles represent catch per unit effort in a research trawl towed at each station. Crosses indicate zero catches. Bars indicate percentages of each regional stock group, from left to right: Japan (downward diagonal), Russia (black), northwestern Alaska (upward diagonal), Alaska Peninsula and Kodiak (white), southeastern Alaska and British Columbia (horizontal brick), on three different survey lines. NPO = North Pacific Ocean, GA = Gulf of Alaska.

in the open ocean, and are still frequently used and cited in the scientific literature. These models need to be updated, however, because they are primarily based on data collected during the mid-1950s to late 1960s, when (1) the North Pacific climate regime was in a different phase than after the 1977 regime shift (Mantua et al. 1997), (2) there were no large-scale releases of hatchery chum and pink salmon into the North Pacific Ocean (Mahnken et al. 1998), and (3) large-scale high-seas driftnet fisheries were harvesting large percentages of salmon returning to Russia and Alaska (e.g., Fredin et al. 1977; Harris 1987). In addition, these old conceptual models do not tell us anything about interannual variation and the effects of ocean conditions on stock-specific distribution and migration patterns.

More recently, researchers have been attempting to develop quantitative models of open ocean distribution and movements of some numerically dominant salmon species and stocks (e.g., Hiramatsu and Ishida 1989; Thomson et al. 1992, 1994; Dat et al. 1995; Rand et al. 1997; Walter et al. 1997; Azumaya and Ishida 2004). For the most part, however, these quantitative models have failed to successfully capture relatively clear differences in the open ocean distribution and migratory orientation of Asian and North American salmon stocks. An added difficulty is that the existing time series of empirical data are usually not sufficient to validate computer models.

We are now in the midst of a genetic revolution that is beginning to provide reliable mid- to small-scale estimates of salmon stock composition needed to develop and validate quantitative models of interannual variation in open ocean

distribution and migration patterns of salmon (see Fig. 3). Chum salmon were the focal species for the initial development of a comprehensive Pacific Rim genetic (allozyme) baseline. These data were used to estimate the stock composition of chum salmon in samples collected during research vessel surveys and to develop new conceptual models of chum salmon distribution and migration patterns for major regional stocks (e.g., Figs. 3 and 4, top panel; Urawa 2000, 2004; Urawa et al. 2001). The results of analyses using 20 allozyme loci from 356 chum salmon populations have shown (1) a higher degree of overlap in the oceanic distribution of Asian and North America stocks than that extrapolated by previous methods, (2) substantial intra-annual fluctuations in stock composition over short time periods, and (3) greater use of the Bering Sea by immature and maturing stocks from throughout the species' range than that indicated by tagging studies (Seeb et al. 2004). Seeb et al. (2004) also suggest that geographically but not genetically similar populations of chum salmon follow similar migration routes.

Our conceptual model of the seasonal migrations of Bristol Bay sockeye salmon (Fig. 4, bottom panel), which incorporates recent data from genetic (DNA) analysis (Habicht et al. 2005), scale pattern analysis (Bugaev 2005), and exploratory fishing (Farley et al. 2005), points to a more extensive distribution of juvenile and immature North American sockeye salmon in the Bering Sea in summer and fall than was indicated by earlier models (Burgner 1991). However, earlier models may accurately reflect seasonal distributions of salmon in the Bering Sea during "cool" periods, because most of the data were collected during relatively cool periods
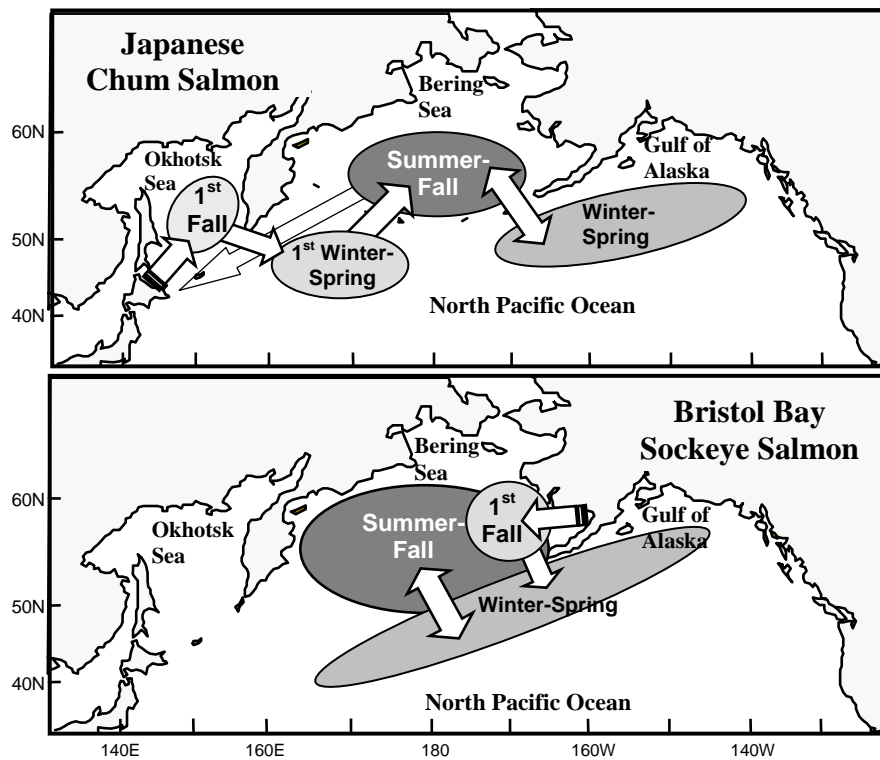
Fig. 4. Examples of seasonal stock-specific migration models for regional stocks of Asian and North American salmon. Top panel: Model for Japanese hatchery chum salmon as estimated by genetic stock identification (Urawa 2000, 2004; Urawa et al. 2001). In their first summer-fall, juveniles are distributed in the Okhotsk Sea. In their first winter, they are distributed in a narrow region of the western North Pacific. By their second summer-fall, they have migrated into the Bering Sea, and in late fall they migrate south and east and spend their second winter in the Gulf of Alaska. In subsequent years, they migrate between their summer-fall feeding grounds in the Bering Sea and their winter habitat in the Gulf of Alaska. In their last summer and fall, maturing fish migrate back to Japan through the western Bering Sea and western North Pacific. Bottom panel: Migration model for Bristol Bay sockeye salmon as indicated by tag recoveries (Myers et al. 1996), scale pattern analyses (Myers et al. 1993, Bugaev 2005), parasite tags (Burgner 1991), genetic (DNA) stock identification (Habicht et al. 2005), and exploratory fishing (Farley et al. 2005). In their first oceanic summer and fall, juveniles are distributed on the eastern Bering Sea shelf, and by the following spring immature salmon are distributed across a broad region of the central and eastern North Pacific. In their second summer and fall, immature fish migrate to the west in a band along the south side of the Aleutian chain and northward through the Aleutian passes into the Bering Sea. In subsequent years, immature fish migrate between their summer/fall feeding grounds in the Aleutians and Bering Sea and their winter habitat in the North Pacific. In their last spring, maturing fish migrate across a broad, east-west front from their winter/spring feeding grounds in the North Pacific, northward through the Aleutian passes into the Bering Sea, and eastward to Bristol Bay.
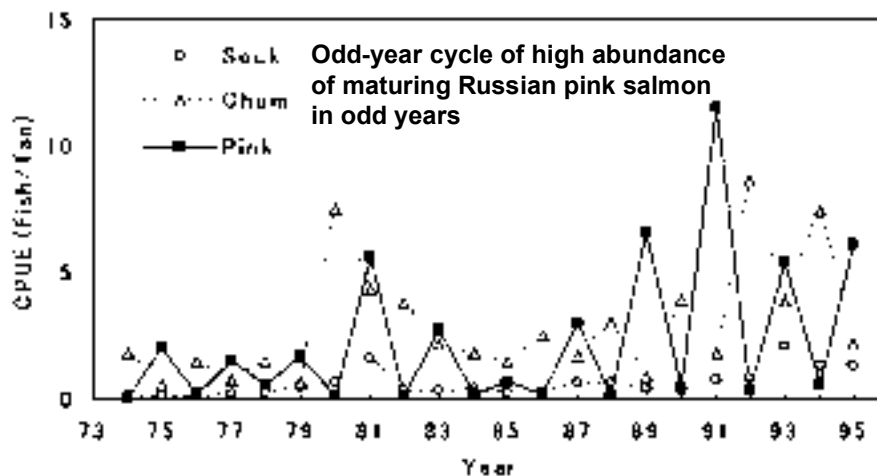
Fig. 5. Example of interannual variation in sockeye, chum, and pink salmon catch per unit effort (CPUE; 1 tan = 50 m of gill net) in Japanese research vessel catches in the Bering Sea. Because of their two-year life cycle (including one winter in the ocean), maturing pink salmon are genetically different in even and odd years. Maturing pink salmon returning to spawn in rivers in eastern Kamchatka, Russia, are the dominant regional stock in the Bering Sea in odd-numbered years. Data and figure source: Ishida et al. 2005.
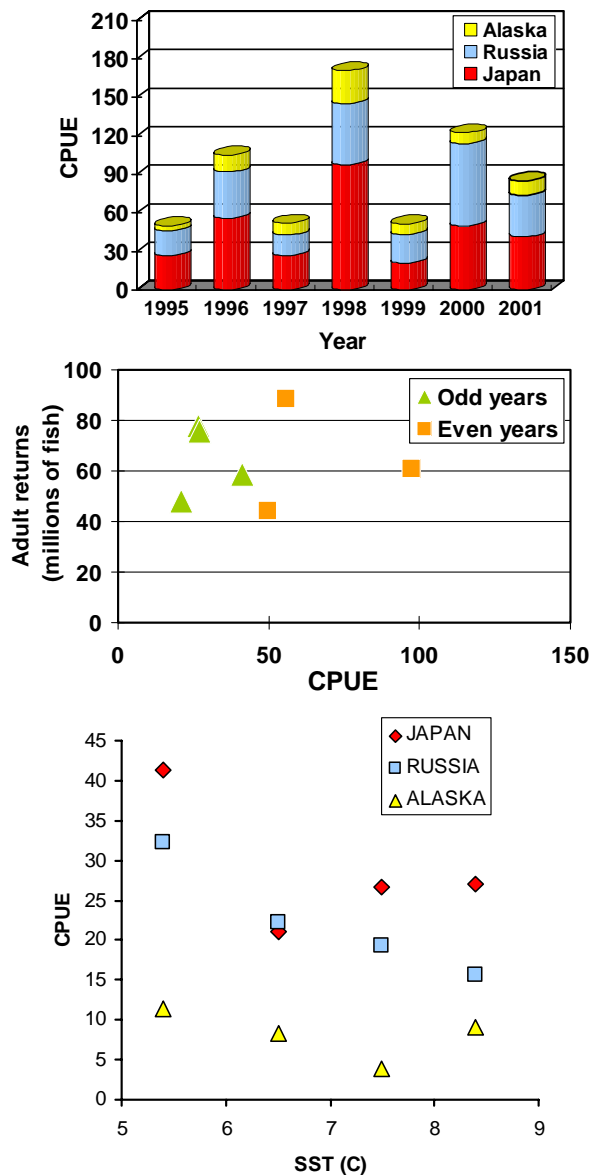
Fig. 6. Top panel: Interannual changes in mean catch per unit effort (CPUE) of maturing chum salmon stocks in research gill nets in the central Bering Sea (180°), July 1995–2001. Center panel: Relation between chum salmon returns to Hokkaido, Japan, and Bering Sea CPUEs of maturing Japanese chum salmon. Bottom panel: Relation between sea surface temperatures (SSTs) and CPUEs of maturing chum salmon stocks in the Bering Sea in July of even years. Data source: S. Urawa, National Salmon Resources Center, Japan.

in the 1950s–60s, while most recent data were collected during a period of warming in the Bering Sea (Khen and Basyuk 2005).

Research vessel catches of salmon in the open ocean vary significantly from year to year (e.g., Fig. 5; Ishida et al. 2002; Ishida et al. 2005). These variations likely result from changes in stock abundance and composition, distribution, migration routes, migration timing, and physical habitat (temperature, salinity, currents, e.g.), as well as prey abundance or distribution. At present, however, time series of ge-

netic stock identification data are too limited to provide detailed information on interannual variation in stock-specific distribution and migration routes in the open ocean. Perhaps the best available genetic (allozyme) data time series describes chum salmon caught in July (1995–2001) in research gillnets in the central Bering Sea (Fig. 6). The strong odd-even year variation in research gillnet catch per unit effort (CPUE) of maturing chum salmon is likely due to a density-dependent change in the salmon's distribution (though not survival) in years when maturing eastern Kamchatka pink salmon were abundant in the Bering Sea, as they generally are in July of odd years (Fig. 6, top panel; Fig. 5; Azumaya and Ishida 2000; Ishida et al. 2002). There is no direct relation between estimated relative abundance of maturing Japanese chum salmon in the central Bering Sea in July and subsequent adult returns to Japan (Fig. 6, center panel). There is a strong negative relation, however, between the relative abundance of Russian chum salmon and sea surface temperatures (SST) in the central Bering Sea in July (Fig. 6, bottom panel). This correlation might reflect the influence of ocean temperature on run timing, i.e., in warm SST years Russian salmon may mature faster and leave the central Bering Sea sooner, resulting in lower CPUEs in July. There is no apparent relation between research gillnet CPUEs of maturing Russian chum salmon in the central Bering Sea in July (Fig. 6) and subsequent adult returns to Russia (commercial catch, see PICES 2004).

Even more effective than allozyme baselines in identifying individual populations, comprehensive DNA baselines for chum salmon and other species are being developed and applied to questions about open ocean distribution and migration patterns of salmon (NPAFC 2004). Unfortunately, this genetic "revolution" is happening at a time when the number of salmon research vessel surveys in the open ocean is diminishing, due in part to decreasing government support for such surveys. Nevertheless, through cooperative research programs coordinated by NPAFC (for example, BASIS, Bering Aleutian Salmon International Survey, 2002-present), we are rapidly advancing in our knowledge of stock-specific distribution and migration patterns of salmon (NPAFC 2005; Urawa et al. 2005).

Interannual Variation in Salmon Distribution Relative to Ocean Conditions

In this section, we will review a case study that sought relations between interannual changes in salmon distribution and ocean conditions. SST is the main index of interannual variation in natural open ocean habitats considered in this section. We do not review other well-known climatic indices, such as ALPI (Aleutian Low Pressure Index) and PDO (Pacific Decadal Oscillation), which are believed to characterize long-term climatic trends over the North Pacific. Ishida et al. (2002) did not find any significant correlation between SSTs and the Aleutian low-pressure index (ALPI)
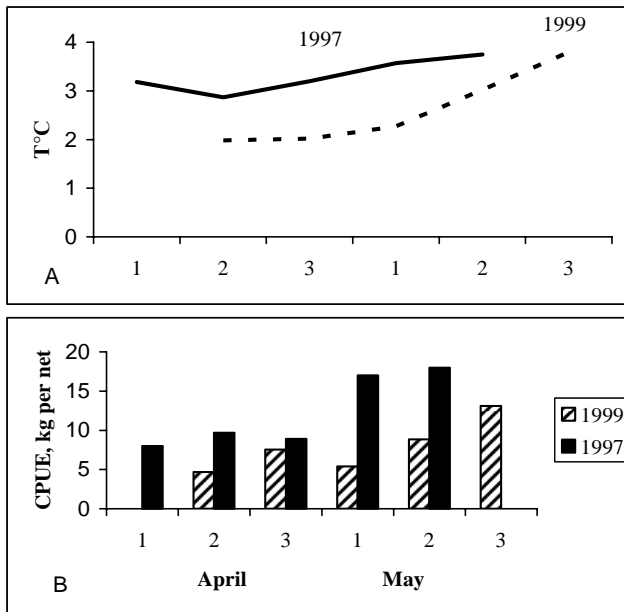
Fig. 7. Comparison of (A) sea surface temperatures (T°C) and (B) salmon catch per unit effort (CPUE, kg of salmon per net) in 1997 and 1999 in the western North Pacific Ocean off Kamchatka in April and May. 1, 2, 3 = 10-day periods in April and May.
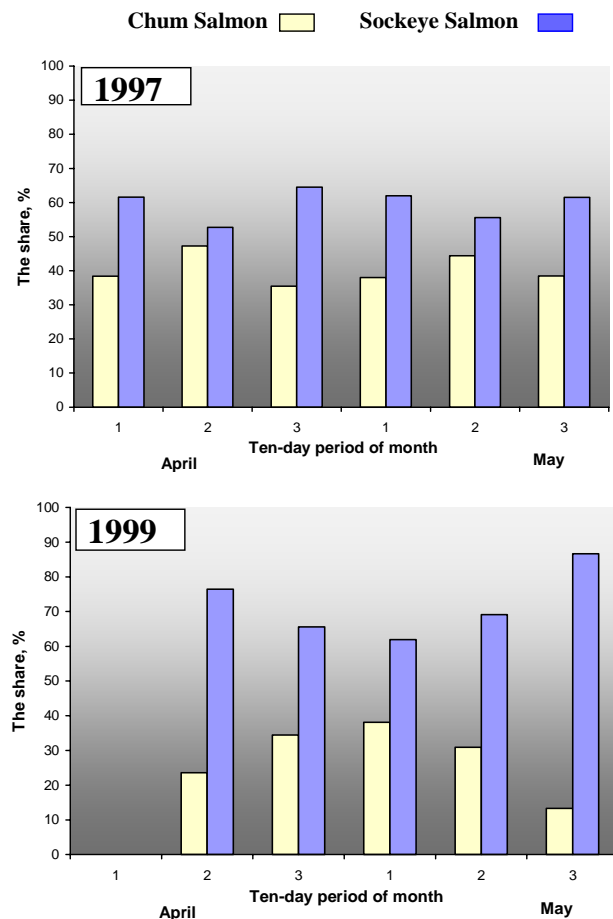

Fig. 8. The share (%) of chum and sockeye salmon in catches made near East Kamchatka during April and May in 1997 and 1999.

or SST and research gillnet CPUEs for each species in the central Bering Sea in July (1970–2000). They speculated that SST, particularly at higher temperatures, causes a shift in salmon distribution that affected their CPUE values.

The major premise of this part of our review is that interannual variation in salmon distribution in the open ocean during the spring-summer season depends largely on ocean conditions during the preceding winter. In particular, spatio-temporal patterns of salmon distribution in spring-summer vary depending on the synoptic type of winter (cold or warm).

The migration routes of salmon in the western North Pacific Ocean in spring appear to follow the northwestward progression of the 2°C SST isotherm (Birman 1985; Erokhin 1990). In years that differ by winter climatic type (cold or warm), the spring CPUEs of salmon in research gillnet catches and corresponding concentrations of salmon in the open ocean vary during the same ten-day period. For example, hydro-meteorological conditions in the western North Pacific in April–May of 1997 and 1999 were quite different. The winter of 1996–1997 was warm. In the first ten-day period of April 1997, the SST in the North Pacific waters off Kamchatka reached 3°C, and by the second half of April-early May 1997, SSTs had already reached 3.5–4°C (Fig. 7). In contrast, the winter of 1998–1999 was cold. In the second half of April 1999, SSTs in the North Pacific waters off Kamchatka had not reached 2°C. By the beginning of May, the surface layer had warmed to 2.3°C. Only by the end of May did the maximum SST reach about 4.0°C, which was lower than the mean long-term values for this period by about 1.5°C. In 1999, the temperature difference between the surface and 100 m below the surface did not exceed 1.0–1.5°C, which is characteristic of the hydrological winter. The low water temperature in spring 1999, compared to the same period in 1997, resulted in fewer salmon in catches in the western North Pacific Ocean off Kamchatka (Fig. 7).

In April–May of 1997 and 1999, three species of salmon (sockeye, chum, and chinook) were caught by research gill nets in North Pacific waters off Kamchatka (Klovach et al. 2000; Klovach 2003). Sockeye and chum salmon were observed during the same period, and chinook salmon appeared in catches in mid May. The ratio of sockeye and chum salmon in the catches was different during warm (1997) and cold (1999) years. The proportion of sockeye salmon was higher in 1999 than in 1997 (Klovach et al. 2000; Klovach 2003; Fig. 8). Sockeye salmon were also the predominant species in North Pacific catches off Kamchatka during subsequent, cold years (2000 and 2001). We hypothesize that this increase in the relative abundance of sockeye salmon was associated with cooling of the western North Pacific Ocean during the second half of the 1990s. At that time, ice cover in waters off the western and eastern coasts of Kamchatka increased, and retreated later in the year (Fig. 9). In the oceanic region where Russian sockeye salmon overwinter (in the North Pacific Ocean, south of the Aleutian Islands), it
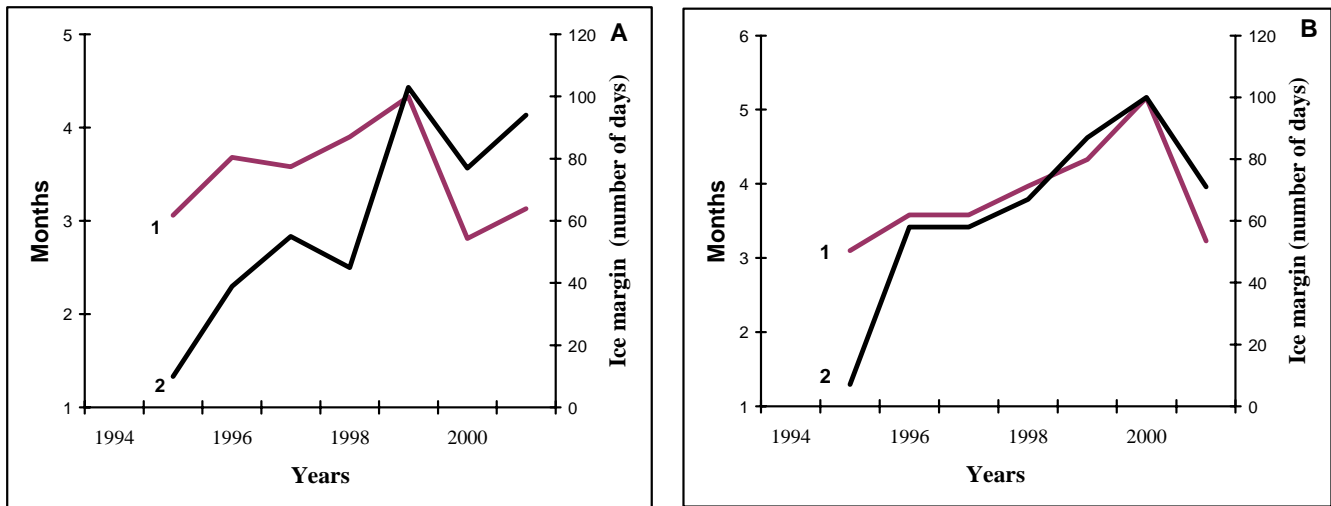
Fig. 9. Trends in sea ice cover in the western North Pacific Ocean off the western (A) and eastern (B) coasts of Kamchatka at 53°N, 1995–2001. 1-date that the sea ice margin crossed 53°N during spring warming. Dates (months): 1 = January, 2 = February, 3 = March, 4 = April, 5 = May. 2-duration (number of days) of sea ice cover at 53°N.
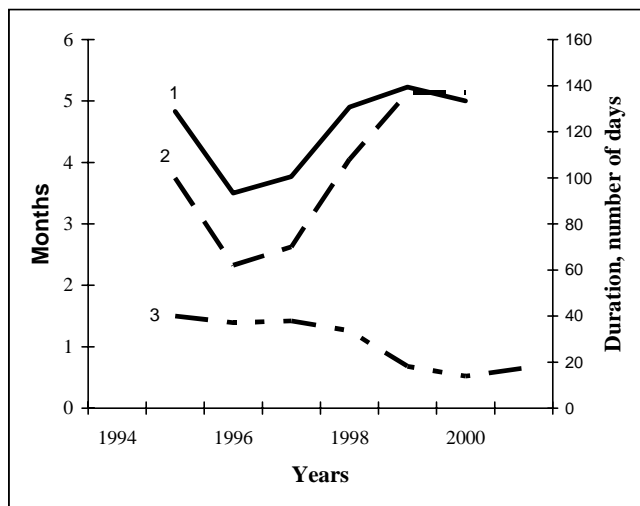
Fig. 10. Trends in the 5°C isotherm in the eastern North Pacific Ocean at 50°N, 170°W during spring warming and autumn cooling: 1-date that the 5°C isotherm crossed 50°N, 170°W when warming; 2-duration of 5°C-isotherm at 50°N, 170°W (number of days); 3-date that the 5°C isotherm crossed 50°N, 170°W when cooling. Dates (Months): 0 = December, 1 = January, 2 = February, 3 = March, 4 = April, 5 = May.
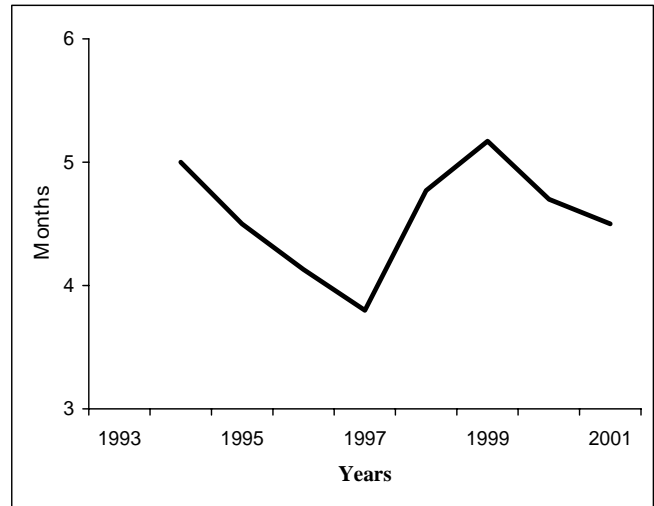
Fig. 11. Interannual variability in the dates that the 2°C-isotherm consistently crossed the line from Bering Island to 51°N, 160°E during spring warming in the western North Pacific Ocean. Dates (Months): 3 = March, 4 = April, 5 = May, 6 = June.

was observed that the cold season lasted longer and spring warming began later in the year (Fig.10).

These cooler conditions apparently caused a delay (compared to mean long-term dates) in the migrations of maturing salmon to the east and west coasts of Kamchatka, a change in the migration routes of sockeye and chum salmon returning to the East Kamchatka coast, and a shift in the oceanic feeding patterns of different salmon species and stocks. In particular, the low temperature of North Pacific waters off Kamchatka in the spring of 1999 and 2000 caused the sock-

eye salmon's main migration routes to shift south by 2–4°, a realignment that coincided with a displaced zone of water with optimal temperatures for sockeye salmon (Gritsenko et al. 2000, 2002; Fig. 11). Instead of migrating across the southwestern Bering Sea, as occurs in warm years, sockeye salmon returning to the Kamchatka River migrated north along the coast of East Kamchatka to the mouth of the river. As a result, not only in May but also in June of 1999 and 2000, the CPUEs of sockeye salmon in North Pacific waters off Kamchatka were higher than in warm years (Gritsenko et
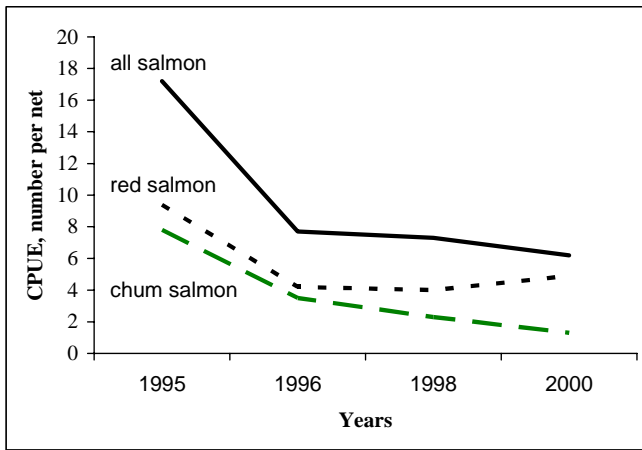
Fig. 12. Catch per unit effort (CPUE, number of fish per net) of salmon in the western North Pacific Ocean off East Kamchatka, June 1995–2000. Red salmon = sockeye salmon.
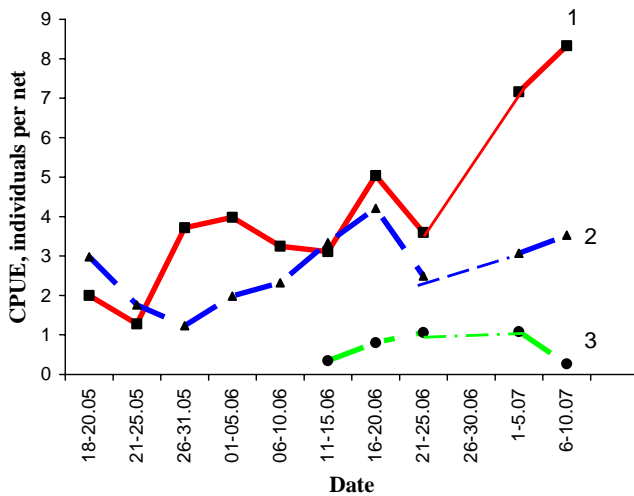
Fig. 13. Catch per unit effort (CPUE, individuals per net) in the western North Pacific Ocean near Kamchatka in 2001. 1 = sockeye salmon, 2 = chum salmon, 3 = pink salmon. Date = days.month, e.g., 18–20.05 is May 18–20, 2001.

al. 2000, 2002; Fig. 12).

Thus, the SST in early spring is a signal, not only triggering migrations of maturing salmon to the coasts, but also determining the rates of these migrations, the schedule of fish maturation, and, eventually, the closing dates of migrations, when salmon enter their natal rivers. In May–June 1997, a water mass with abnormally high temperatures formed in the area of the North Kuril Straits. This abnormal formation produced earlier migrations of West Kamchatka sockeye salmon stocks into the Sea of Okhotsk, compared to mean long-term dates. In contrast, in 1999–2001, warming of western North Pacific waters adjacent to the North Kuril Straits began late and continued until the end of June-mid July. As a result, West Kamchatka sockeye salmon remained in North Pacific waters off East Kamchatka longer than in previous years, and high CPUEs of sockeye salmon were observed in that area in early July 2001 (Fig. 13).

In warm years, pink salmon appear in North Pacific waters off Kamchatka in early June, and by mid June, research gillnet catches are relatively high. For example, in 1997 and 1998 (warm years), a few individual pink salmon were caught in early June (June 2) in Pacific waters off Kamchatka, while more than 4 t/day of an approximate total 10 t were caught in mid June (June 12). In 2001 (a cold year), only a few individual pink salmon were caught off East Kamchatka in mid June (June 15), but one t of a total 12 t was caught on July 4.

In years with different thermal conditions, the relative abundance of salmon species likewise varies spatially. For example, in warm years pink and chum salmon predominate numerically in the open ocean off east and west Kamchatka in late June-early July, while most sockeye salmon have already migrated from the area. In cold years, the ratio among these three salmon species changes due to the delayed migrations of West Kamchatka sockeye salmon in North Pacific waters and the later appearance of pink salmon. At these times, sockeye salmon predominate in North Pacific catches made off Kamchatka until the second ten-day period in July.

The conditions observed in 2003 provide a clear illustration of the effect of winter habitat conditions on the distribution and biological characteristics of salmon during the spring-summer season. An analysis of SST distribution in the southwestern Bering Sea during winter of 2002–2003 showed that January 2003 was a relatively warm month. In subsequent winter months, SSTs neared mean long-term values, and, as a result, overall ice conditions changed. Later, the processes of ice erosion exceeded the mean long-term dates by 8–14 days. This extended ice erosion was associated with both cyclonic activity and the advection of warm and wet air masses from March to April. A standard hydrological survey in the southwestern Bering Sea in mid-June found that the temperature of the upper 10-m water layer was the highest measured over the previous six years. From May to June 2003, SSTs in the western and eastern North Pacific were 3–5°C higher than the mean long-term values for the time period. Due to the earlier warming of these water masses, pink salmon appeared in research gillnet catches off east Kamchatka as early as the beginning of June, and peak CPUEs of pink salmon occurred by the end of June, as one would expect in a warm year.

We assume that the interannual differences in research gillnet CPUEs observed in our case study are not related to differences in the vertical distribution of salmon. In general, salmon are distributed at the surface of the open ocean at night (Walker et al., 2007). The nocturnal distribution of salmon was confirmed by Klovach and Gruzevich (2004), who set research gill nets at the ocean surface at night, and retrieved them 9–12 hours later. Welch et al. (1995, 1998) found abrupt decreases in the relative abundance (CPUE) of salmon in research vessel catches (using gill nets, longlines,
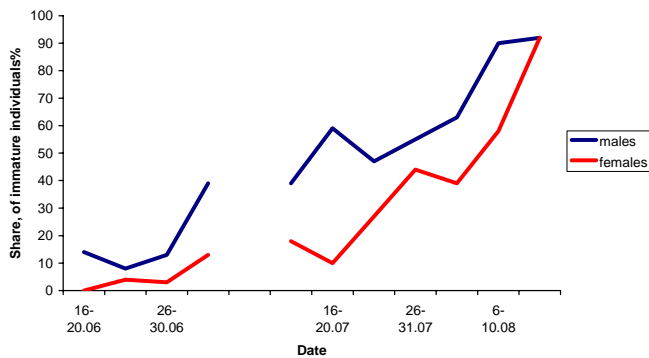
Fig. 14. Share of immature sockeye salmon in the western North Pacific Ocean near Kamchatka, 2003. Date = days.month, e.g., 16-20.06 is June 16-20, 2003.

and rope trawls) when SSTs were at or near the upper thermal limit for salmon habitats. However, we do not know if this decrease in abundance resulted from a change in the vertical or horizontal distribution of salmon. Our knowledge is limited because SSTs in our case study were not at the upper thermal limit of salmon distribution in the North Pacific Ocean.

Climatic conditions in 2003 (warm winter, early spring) also affected the biological characteristics of salmon, particularly the degree of gonad maturity. Because of high water temperatures, salmon matured faster in 2003 than in 2001 or 2002. Maturing salmon migrated to their spawning grounds sooner and immature fish occupied open-ocean feeding grounds (previously occupied by maturing fish) earlier than usual. As a result, in 2003 a large number of immature salmon were caught in North Pacific waters off Kamchatka as early as June, and in July, about 40% of the catch in these regions was immature male sockeye salmon (Fig. 14). In cold years, the same situation occurs at least two weeks later (Klovach and Gruzevich 2004). Thus, taking into consideration the correlation between synoptic type of winter (cold or warm) and migration patterns, it seems possible to forecast the distribution of salmon in the open ocean during their pre-spawning migrations, as well as the dates of their migrations to spawning grounds.

We conclude that many measures of interannual variation in salmon populations in the open ocean (e.g., the number of sockeye and chum salmon in catches, the date when immature individuals appear on pre-spawning feeding grounds, the degree of gonad maturity, the ratio between male and female individuals, and the date when pink salmon appear in catches made in Pacific waters off Kamchatka) are determined to a large extent by climatic conditions.

Hodgson et al. (2006) recently evaluated a similar model developed by Blackbourn (1987) for North American sockeye salmon. Blackbourn hypothesized that interannual variation in the timing of adult sockeye salmon returns to rivers in North America is related to winter-spring SSTs in the Gulf of Alaska. According to this hypothesis, maturing
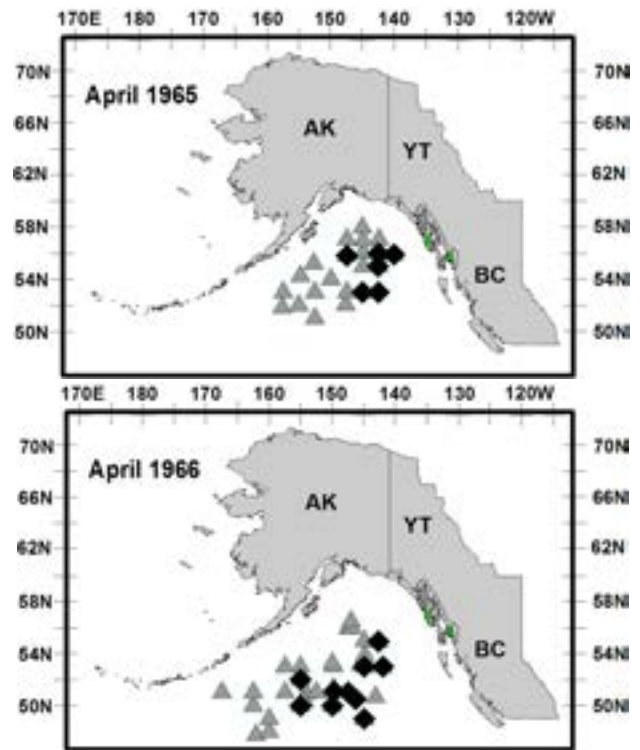
Fig. 15. Example of annual variation in stock-specific distribution of maturing sockeye salmon in the Gulf of Alaska in the spring (April 1965 and 1966), as shown by historical tagging experiments (n = 193 fish). The symbols indicate the high seas release locations of tagged fish later recovered in western Alaska. Western Alaska (Bristol Bay) = closed (grey) triangles and southern British Columbia (Fraser R.) = closed (black) diamonds. Note that while both stocks are distributed across broad fronts, and distributions of the two stocks overlap significantly; Bristol Bay sockeye salmon are distributed farther to the west and north than southern British Columbia fish. Using the Southern Oscillation Index criteria, it can be determined that 1964–65 was a moderate La Niña (cold) winter and 1965–66 was an El Niño (warm) winter. AK = Alaska, YT = Yukon Territory, BC = British Columbia. Data source: High Seas Salmon Research Program, University of Washington, Seattle.

North American sockeye salmon in the Gulf of Alaska are distributed farther to the north and west in warm winters than in cool winters. If swimming speeds and start dates of return from the open ocean are constant, then salmon runs in southeastern rivers (e.g., Fraser River, BC) will be late, and runs in rivers farther to the north and west (e.g., Bristol Bay, Alaska) will be early. In general, the results of Hodgson et al. (2006) indicated that (1) correlations between migratory timing and SST are reversed for northern and southern populations, (2) interannual variation in salmon distribution and sea temperature are related, and (3) the start-of-return date is a population-specific trait that is not affected by location at sea.

There are little or no empirical data on salmon migrations in the Gulf of Alaska to validate Hodgson's results. Almost all high seas tagging research in the Gulf of Alaska was carried out during the 1960s, but oceanographic conditions in that decade were irregular—particularly in the winter and

spring of 1966, when northward transport was about 50% of the 10-year average, summer wind stress conditions existed in February, and all westward flow of warm water in the Alaska Stream was apparently re-circulated in the Gulf of Alaska (Favorite et al. 1967). Thus, data retrieved in those years do not conform to expectations. Using the Southern Oscillation Index criteria, it can be determined that 1964–65 had a La Niña (cold) winter and 1965–66 an El Niño (warm) winter (http://www.wrcc.dri.edu/enso/reanlnen.html). In the spring of 1966, salmon were distributed farther offshore to the south and west than they were in the spring of 1965 (IN-PFC 1967a, b). Limited tag data suggest that both northern (Bristol Bay) and southern (Fraser River) sockeye salmon stocks may be displaced to the south and west, rather than north and west, in the spring following a warm winter (Fig. 15). Additional research is needed to develop and validate models to predict the effects of climatic forcing on stock-specific open ocean distribution and run timing of salmon.

Interannual Variation in Ocean Conditions in the Gulf of Alaska and the Bering Sea

In summer, interannual variation in the relative abundance of salmon in the Bering Sea appears to be inversely related to that of salmon in the Gulf of Alaska (Ishida et al. 2002). This relation might be driven at least to some extent by SSTs or other oceanographic conditions in the Gulf of Alaska, e.g., chum and sockeye salmon are more abundant in the Bering Sea than in the Gulf of Alaska in years when sum-

mer SSTs are high in the Gulf of Alaska (Ishida et al. 2002). In this section we review information on interannual variation in ocean environments where salmon stocks are distributed. The basic premise of this part of our review is that the circulation and climate in the North Pacific Ocean and Bering Sea are interconnected. Another premise is that the oceanographic conditions in these regions have been changing significantly over the past several decades, even prior to the regime shift of 1977 (Mantua et al. 1997).

The 1977 regime shift was a large-scale climatic event, and can be seen in much of the environmental data for the region, as illustrated in Mantua et al. (1997). That study focused on SST, because that measurement was the ubiquitous data set, though not necessarily the "best" data to explain salmon variability. Unfortunately, other oceanographic data are sparse. Long-term series of small- to mid-scale data are absent. We must, therefore, deal with the few large-scale and long-term data series that are available. For the northeastern Pacific Ocean and Gulf of Alaska, data sets include hydrographic measurements taken at Ocean Station P (OSP; 50°N, 145°W) since 1958 (Freeland et al. 1997); coastal observations of sea level; measurements of surface temperature and salinity taken at Canadian lighthouses along the British Columbia coast, some from early in the last century (Freeland, http://wlapwww.gov.bc.ca/air/climate/indicat/pdf/seasurftemp-tdoc1.pdf); hydrographic observations made at Gulf of Alaska Station 1 (GAK1, 60°N, 149°W) from 1970 to the present (Royer 2005); and observations of currents, temperature and salinity per depth, taken since 1995 from
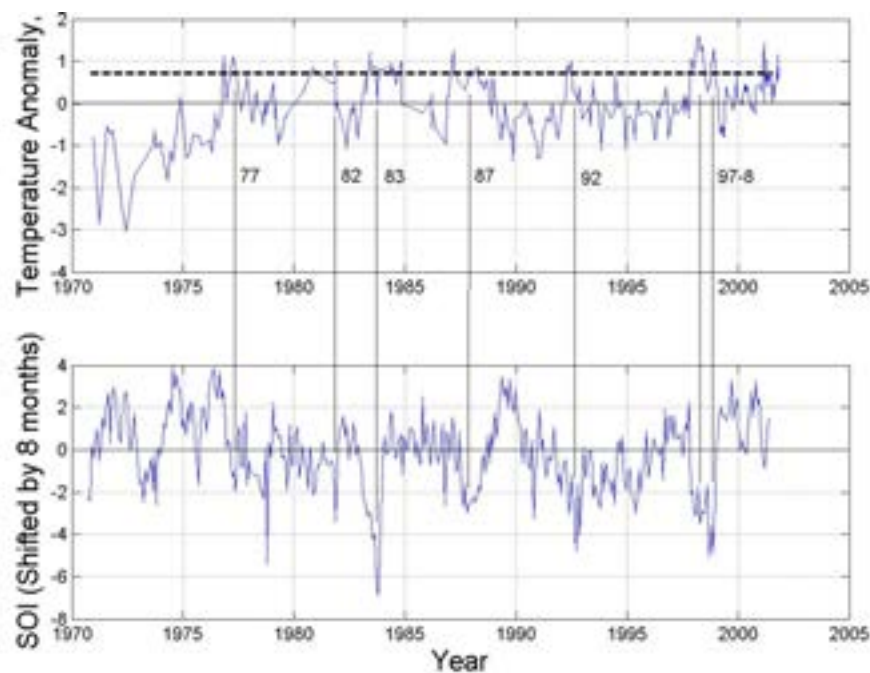
Fig. 16. Gulf of Alaska (GAK1) temperature anomalies at 150 m (°C, upper panel) with SOI (lower panel) since 1970 with responses to ENSO events noted by vertical lines between panels. There is a 99% correlation between data sets with a C.I. linear trend of 0.03°C increase/year at 150 m and throughout the water column (250 m). From Fig. 14 in Royer (2005): "One standard deviation is indicated with dashed line." ENSO = El Niño-Southern Oscillation, SOI = Southern Oscillation Index.
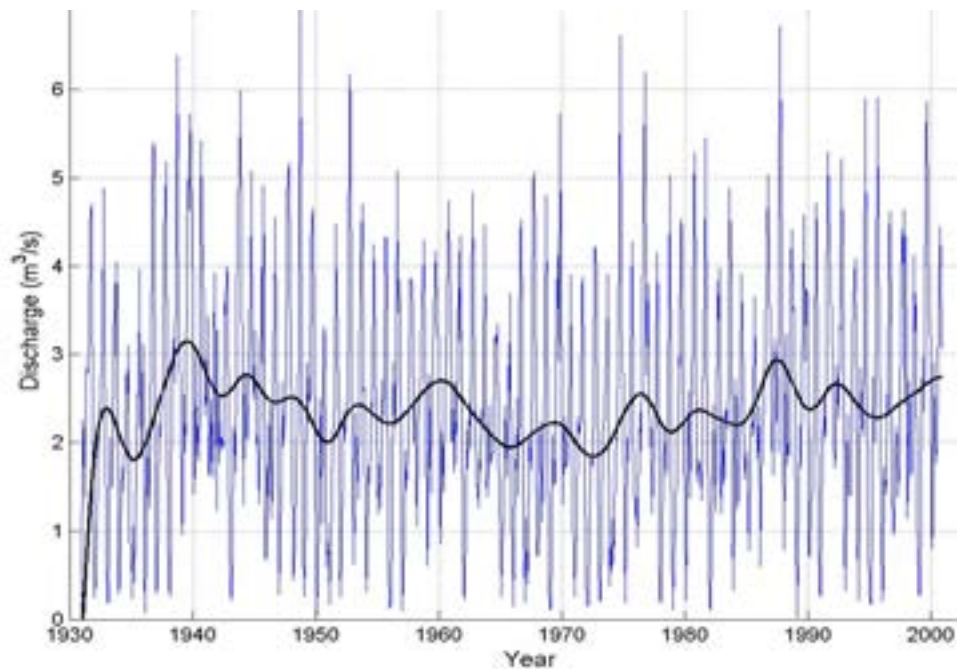
Fig. 17. Monthly coastal freshwater discharge for the Gulf of Alaska from the Alaska-B.C. border to Cook Inlet. From Fig. 5 in Royer (2005): "Heavy line is 5-year filtered (Butterworth) discharge." Note that this volume exceeds that of the Mississippi River's 14,400 cubic meters per second.

moorings at Site M2 on the 70-m isobath in the southeastern Bering Sea (Stabeno et al. 1995, 2001, 2002a).

King et al. (2005) summarized oceanographic changes in the region since the 1998 regime shift. These changes include increased storm activity and increased mixed layer depth in the Gulf of Alaska as the region returned to cooler, stormier conditions. The Bering Sea and Aleutian Islands apparently remained unaffected by these cooler conditions, instead warming and losing their ice cover. Recent climate variability over the North Pacific Ocean and Bering Sea support the idea that these regions might be linked together (King et al. 2005).

Gulf of Alaska

In winter, the depth of the mixed layer at OSP has been decreasing, which suggests that the supply of nutrients into the euphotic zone will also diminish (Freeland et al. 1997). This shoaling of the mixed layer is the result of a general warming and freshening of the ocean's upper layer, as observed at OSP and along the British Columbia coast (H.K. Freeland, http://wlapwww.gov.bc.ca/air/climate/indicat/pdf/seasurftemp-tdoc1.pdf). Increased wind stress over the Gulf of Alaska is expected to deepen the wintertime mixed layer, but apparently diminished density in the upper layer counteracts the tendency toward increased wind mixing. Long-term hydrographic measurements at GAK1, farther north, support the findings of Freeland's coastal measurements. A significant temperature increase of 0.03°C per year has been found throughout the entire water column (250 m) near Seward, Alaska (Royer 2005; Fig. 16). The salinity of the upper

layer (0–100 m) is also diminishing in response to increased coastal precipitation and freshwater discharge since 1970 (Fig. 17). Unlike OSP, this coastal site has not displayed any significant trends in wintertime, mixed-layer depths since 1970 (Sarkar et al. 2005)

Therefore, the major changes that have been taking place in the physical oceanography of the Gulf of Alaska include: a relatively steady increase in the coastal water temperature of the upper layers, a decrease in the mixed-layer depth at OSP (Freeland et al. 1997), an increase in storminess in the Gulf of Alaska, and a decrease in the upper-layer salinity, resulting from increased precipitation and coastal freshwater discharge. This stratification is also enhanced by rapid glacial melting in coastal Alaska (Arendt et al. 2002). Increased stratification will inhibit the flux of nutrients into the upper euphotic zone, trap organisms in that upper layer, increase the amplitude of upper-layer seasonal temperature changes and advance the timing of the spring bloom. Oceanic stratification is taking place in concert with increased wind stress, a force that could counteract the increased stability in new ocean layers. The increased circulation in the Gulf of Alaska as a result of increased stratification and wind stress could also produce more eddies along the shelf break. We do not have enough long-term data on eddy dynamics to determine whether this last conjecture is true.

Bering Sea

In contrast with the Gulf of Alaska, the Bering Sea has very little precipitation, and wind stress has diminished since the 1997–98 regime shift (Wirts and Johnson 2005). As dis-
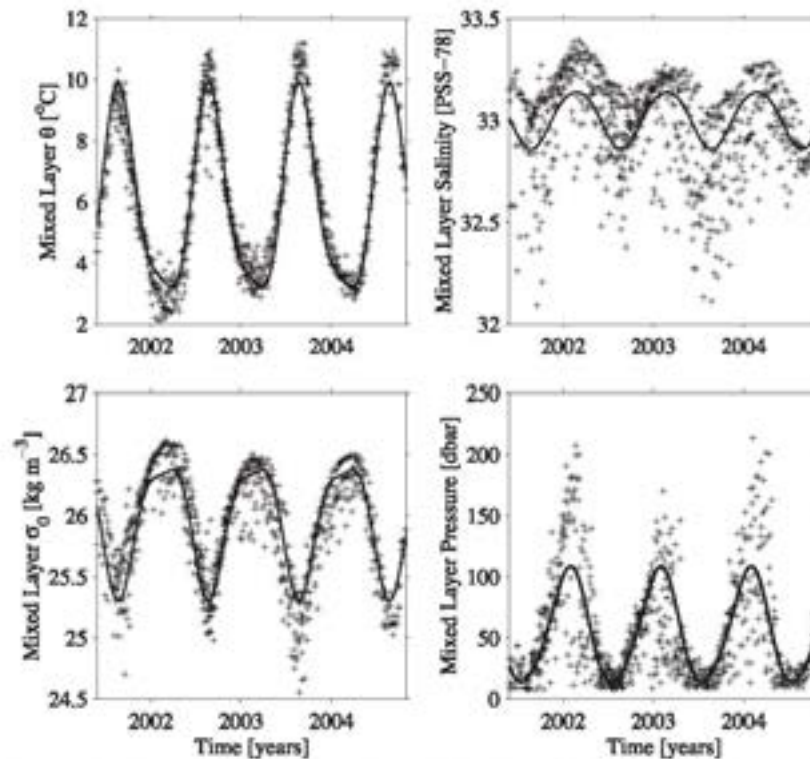
Fig. 18. Mixed layer changes in the Bering Sea from June 2001 to September 2004. From Fig. 2 in Wirts and Johnson (2005): "Mixed-layer potential temperature (top left), salinity (top right), potential density anomaly (bottom left), and pressure at the base of the mixed layer (bottom right) plotted versus time using the float CTD data (plusses) in the southeast Aleutian Basin with seasonal cycles (solid lines) estimated from annual and semiannual harmonics fit to these data."

cussed in the previous section, the inflow of relatively warm water from the Gulf of Alaska will lead to increased stratification and enhanced surface and upper-layer water temperatures. Increased stratification will produce wider variation in seasonal temperatures due to solar heating. Interannual changes in the mixed layer in the southeast Bering Sea from 2001 to 2004 (Fig. 18) reveal an increase in the temperature of the mixed layer, accompanied by a decrease in water salinity and density (Wirts and Johnson 2005), a shift that is consistent with the changing upstream conditions in the Gulf of Alaska.

Changes in seasonal signals such as temperature, sea ice, and winds, will affect salmon production in the Bering Sea (Hunt et al. 2002; Fig. 19). The timing and quality of the spring bloom is highly dependent on the presence of winds and sea ice in early spring. When sea ice is present in or after late March, a strong bloom takes place as the ice retreats. If there is no ice or the ice retreats before late March, the bloom takes place in May or June. In addition to sea ice, eddies apparently play an important role in migration patterns, though eddy dynamics and formation are imperfectly known (Stabeno et al. 2002a, b).

In summary, it appears that upper-layer water temperatures, stratification, and wind stress are increasing, while salinities are decreasing (Gulf of Alaska only). Although the influence of these mid-scale features is yet to be determined,

eddies may play a major role in salmon productivity. Continued satellite altimetry will provide enhanced eddy statistics in the future, perhaps shedding light on this question.

CONCLUSIONS

At present our data are insufficient to answer the question, "What does annual variation in open-ocean salmon stock composition tell us about environmental conditions on small- to mid-size scales?" We conclude from our brief review, however, that climate-driven change in oceanographic conditions in open-ocean feeding areas and along migratory routes of Asian and North American salmon can result in predictable differences in the distribution and migration patterns of salmon.

Clearly, advancement in our knowledge of stock-specific ocean distribution and migration patterns is vital to understanding the status of Pacific salmon in marine ecosystems. Updated models of ocean distribution and migration are needed for most of the major regional stock groups of salmon originating from rivers in the North Pacific Rim.

Pacific salmon species have evolved over millions of years to take advantage of different ecological niches in the open ocean. The diversity of these natural adaptations by numerous individual populations has provided salmon species as a whole with a resilient buffer to the effects of environ-

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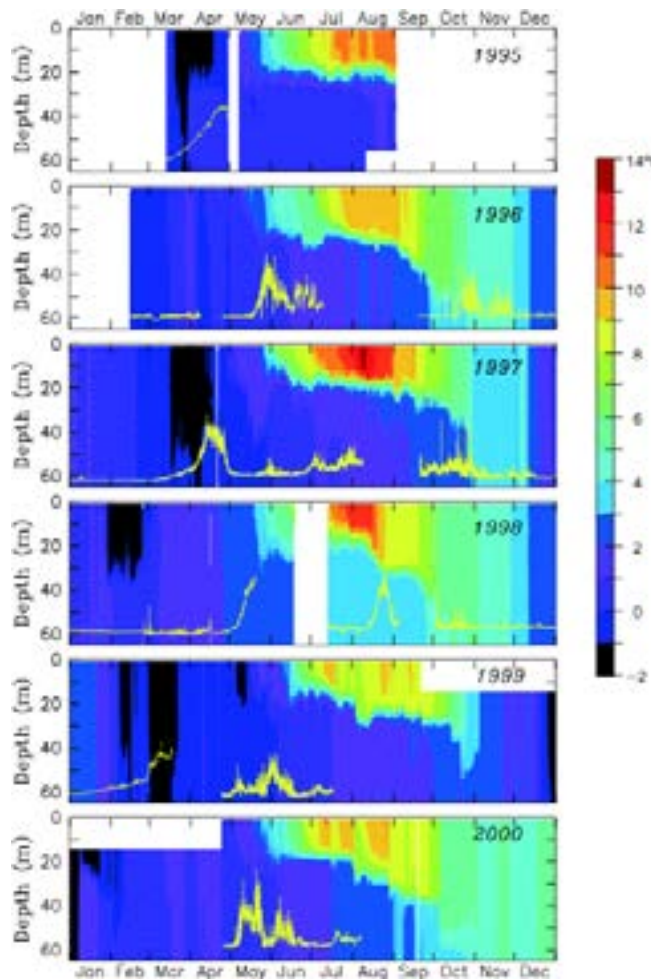Arendt, A.A., K.A. Echelmeyer, W.D. Harrison, C.S. Lingle, and V.B. Valentine. 2002. Rapid wastage of Alaska glaciers and their contribution to rising sea level. Science 297: 382–386.

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Fig. 19. Water column temperatures from the M2 mooring in the middle domain of the Bering Sea, 1995-2000. From Fig. 6 in Hunt et al. (2002): "Areas of black indicate cold water resulting from the presence of melting sea ice. The yellow line near the bottom of each panel indicates fluorescence at 11–13 m. For each year, fluorometer traces have been scaled to the highest value in that year. Gaps in the fluorometer record are the result of fouling of the instrument. When ice is present in or after late March, a strong fluorescence peak occurs as the ice retreats (1995, 1997). When there is no ice (1996) or the ice retreats before late March (1998, 2000), an open-water bloom occurs in May or June. In 1999, the spring was stormy and ice recurred in May. There was a bloom in late March, and another weak and prolonged period of production in late May and June."

mental change on their marine growth and survival. Changes in climate, oceanic conditions, and migration patterns of salmon in the open ocean are inextricably intertwined, and improvements in our ability to make predictions about salmon may very well improve our ability to make predictions about the environment. Global warming is resulting in more frequent and unpredictable environmental changes in open-ocean habitats through which salmon migrate. We conclude that changes in the distribution and migration of indicator stocks of adult salmon returning from the open ocean might provide an "advance warning" of interannual changes in North Pacific marine ecosystems.

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Regional and Seasonal Differences in Temperature and Salinity Limitations of Pacific Salmon (*Oncorhynchus* spp.)

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Abstract: The thermal limitations of the distribution of Pacific salmon (*Oncorhynchus* spp.) in relation to sea surface temperatures are well known. We reanalyzed data on salmon distribution and hydrographic measurements, and estimated the limitations of salmon distribution using T-S diagrams. There was a clear relationship between salmon distribution and salinity in the offshore waters of the North Pacific. The upper thermal limit was 13.3°C for sockeye (*O. nerka*), 15.6°C for chum (*O. keta*), 16.6°C for pink (*O. gorbuscha*), 15.7°C for coho (*O. kisutch*) and 13.4°C for chinook (*O. tshawytscha*). The lower thermal limit was 3.3°C for sockeye, 2.7°C for chum, 2.8°C for pink and 3.7°C for coho salmon, respectively. The upper halo-limit was 33.46 psu for sockeye, 34.45 psu for chum, 34.37 psu for pink, 34.26 psu for coho and 33.95 psu for chinook salmon, respectively. The range of thermal and halo-limits for the pink salmon distribution was wider than those of the other species. The range of these parameters for sockeye salmon was narrower than those of the other species. In winter and spring, the southern limit of salmon distribution in the western North Pacific was dependent on the halo-limit. In the eastern North Pacific, the southern limit was dependent on the thermal limit. In summer and autumn, the thermal limit for sockeye salmon was similar to the southern limit for sockeye in the North Pacific. The occurrence of the halo-limit results in seasonal and regional differences in sea temperature at the southern limit of salmon distribution.

Keywords: Pacific salmon, thermal limit, halo-limit, distribution

INTRODUCTION

It is known that Pacific salmon (*Oncorhynchus* spp.), sockeye (*O. nerka*), chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*) and chinook (*O. tshawytscha*) are widely distributed in the North Pacific Ocean and adjacent waters. The distributions of these Pacific salmon in offshore waters are affected by both physical factors (temperature and salinity, e.g.) and biological factors. Of the five principal salmon species, sockeye prefer the lowest temperatures although there is considerable overlap with the other species (Manzer et al. 1965; Burgner and Meyers 1983). Manzer et al. (1965) showed that the temperature range in northwestern Pacific waters in winter was 1.5–6°C for sockeye. The southern and eastern limit of sockeye distribution in the North Pacific Ocean in winter was between the 6 and 7°C isotherms. In summer, the southern distribution of salmon in the northwestern North Pacific is approximately along the 13.5°C isotherm. Welch et al. (1995) showed that there were thermal boundaries in the distribution of salmon in the eastern North Pacific in spring. On the other hand, there was an obvious relationship between salmon distributions and salinity in offshore waters in the North Pacific (Favorite and

Hanavan 1963; French et al. 1976; Welch et al. 1995; Welch et al. 1999). Thus, we reanalyzed data on salmon distribution and hydrographic measurements simultaneously.

MATERIALS AND METHODS

To assess the salmon distribution, we considered only data sets where fishing and hydrographic measurements were carried out simultaneously. These data were obtained by the Japanese salmon research vessels, *Kaiyo maru*, *Hokko maru*, *Wakatake maru* from 1991 to 2003, the Hokkaido University training ships *Oshoro maru* and *Hokusei maru* from 1978 to 2002, and the Russian research vessel, R/V *TINRO* in 2003. Fishing gear consisted of non-size-selective research gillnets with 10 different mesh sizes, except for the *Kaiyo maru* and the R/V *TINRO* which used surface trawls. The research objectives of the *Kaiyo maru* and the R/V *TINRO* programs were to determine the ocean distribution of salmon as part of the Bering-Aleutian Salmon International Survey (BASIS) program, which was to understand the effect of environmental factors on distributions of Pacific salmon in the Bering Sea. The research objectives of the programs of the *Hokko maru*, *Wakatake maru*, *Oshoro maru* and *Hokusei maru*

were to monitor Japanese salmon. Observations were made mainly from June to September but data from December to February were also included. Although the locations of the observations were different in each season, they covered the entire North Pacific (Fig. 1). Historical data collected from Japanese salmon research vessels in the offshore waters of the North Pacific Ocean from 1972 to 2001 were used to examine the factors limiting salmon distribution.

Water column properties were defined by the vertical profiles of temperature and salinity for each observation. There are major fronts, the Subarctic Front (4°C isotherm at 100-m depth) and the Subarctic Boundary (34.0 psu at 0 m) in the North Pacific (Favorite et al. 1976). These fronts have the axis of the broad eastward flows. The four areas were divided by water properties as follows: the Subarctic Current System which occurs on the north side of the Subarctic Front, the Transition Domain which is the zone between the Subarctic Front and the Subarctic Boundary, the Subtropical Current System which occurs on the south side of the Subarctic Boundary, and the Alaska Current System in the Gulf of Alaska (Fig. 1). The relationship between water properties and salmon distribution was examined using data at 10 m depth in T-S diagrams. The 10-m depth was chosen because daily mixing and precipitation were evident in the upper 10 m of the water column and salmon were distributed in the upper 40 m of the water column (Ogura and Ishida 1995; Walker et al. 2000; Azumaya and Ishida 2005). Monthly mean values for temperature and salinity with a resolution of 1° latitude by 1° longitude, were supplied by the National Oceanographic Data Center (NODC 1994).

The upper and lower limits of temperature and salinity

from locations where salmon were not caught were examined using T-S diagrams. In this study, we define them as the upper thermal limit and the lower thermal limit, and as the upper halo-limit and the lower halo-limit, respectively.

RESULTS

Figure 2 shows the characteristics of water masses at 10 m depth for each station, and whether salmon were caught. Chum salmon were not caught at temperatures above the red line (15.6°C) and below the blue line 2.7°C, and they were not caught at salinities to the right of the purple line (34.45 psu) (Fig. 2a). In this study, we define the temperatures indicated by the red and blue lines as the upper thermal limit and the lower thermal limit, respectively. The salinity indicated by the purple line is defined as the upper halo-limit. Areas that are enclosed by the thermal and halo-limits in the T-S diagram indicate acceptable thermal and halo-limits for chum salmon. This result showed that chum salmon were widely distributed from the Subarctic Current System to the Subtropical Current System. Relatively high densities of chum salmon were seen at salinities < 33.25 psu. Relatively high densities of sockeye were seen at < 33.25 psu, similar to chum salmon (Fig. 2b). However, sockeye salmon were not caught at salinities > 33.46 psu. The halo-limit, 33.46 psu for sockeye salmon, was much lower than that for chum salmon. Sockeye salmon were distributed in the Subarctic Current System and the Alaska Current System. In other words, they were not distributed in the southern part of the Transition Domain and the Subtropical Current System.

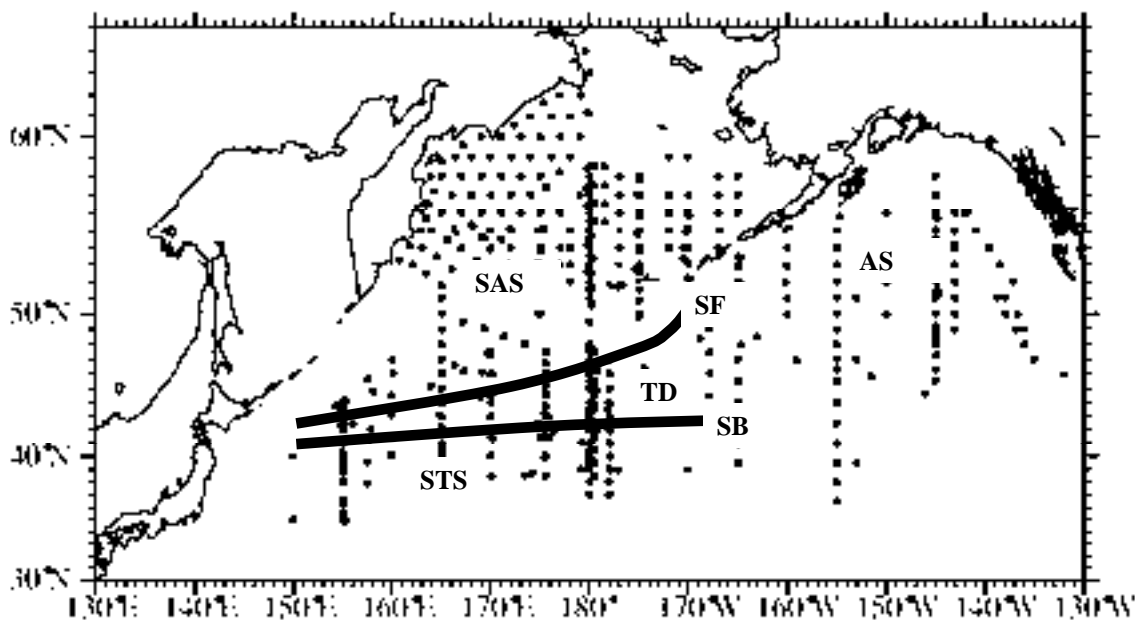Using a similar method, thermal and halo-limits for

Fig. 1. Map of locations of fishing and hydrographic measurements and schematic view of four current systems: Subarctic Current System (SAS), Transition Domain (TD), Subtropical Current System (STS), and Alaska Current System (AS), and two fronts: Subarctic Front (SF) and Subarctic Boundary (SB).
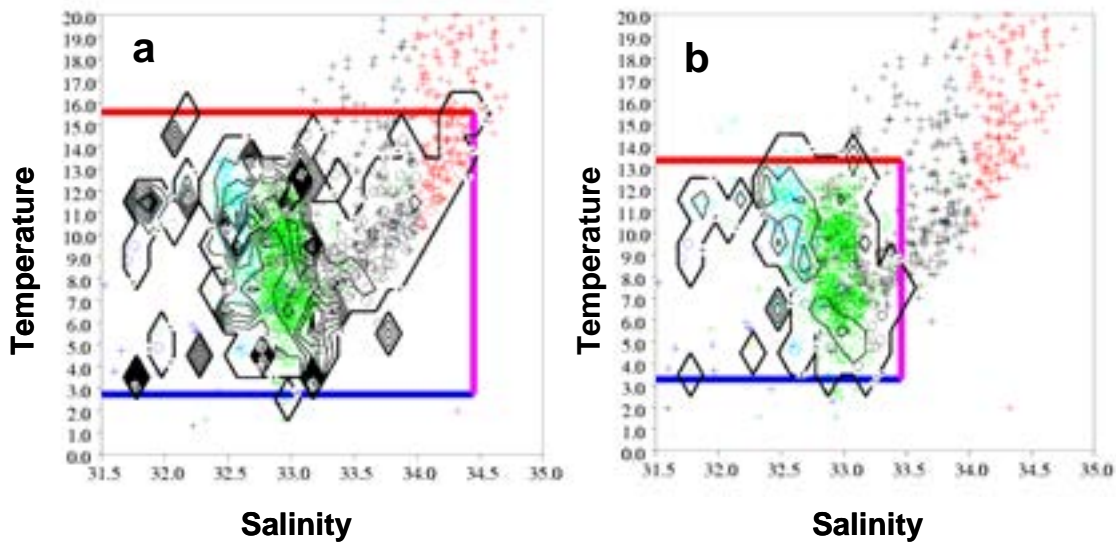
Fig. 2. Results of fishing operations as T-S diagrams with the upper thermal limit (red line), the lower thermal- limit (blue line) and the upper halo-limit (purple line) for chum salmon (a) and sockeye salmon (b). Crosses indicate no catch, and circles indicate catch. Green is the Subarctic Current System, black indicates the Transition Domain, red indicates the Subtropical Current System, and blue indicates the Alaska Current System. Contour indicates CPUE of salmon (number of fish per 30-tan research gillnets or 1-h trawl) at intervals (thin black line) of 20 fish.

pink, coho and chinook salmon are shown in Fig. 3. Vertical profiles for temperature and salinity from depths of 10 to 1000 m at each station are also shown in the T-S diagram. For all species, a lower halo-limit was not detected, and the lower thermal limit for chinook salmon was < 1.6°C. The thermal and halo-limits by species are listed in Table 1. The range of the thermal and halo-limits for pink salmon was wider than that for other species. The range for sockeye salmon was narrower than that of other species. Pink salmon were widely distributed from the Subarctic Current System to the Subtropical Current System, similar to chum salmon. Lower thermal limits for coho salmon were higher than those for other species. The upper thermal limit for coho salmon was similar to those for chum and pink salmon. The upper halo-limit for coho salmon was lower than those for chum and pink salmon. Chinook salmon were distributed from the Subarctic Current System to the Transition Domain. The upper thermal limit for chinook salmon was similar to that for sockeye salmon.

We compared the thermal and halo-limits for sockeye salmon using historical catch data for spring and summer (Fig. 4). We found that in spring, sockeye salmon were not distributed south of the halo-limit (thick line), and that in summer they were not distributed south of the thermal limit (thin line). These results indicate that the thermal and halo-limits estimated in this study are appropriate as the distributional limits for the seasonal and latitudinal distribution of salmon.

Figure 5 shows the horizontal distribution of the acceptable thermal and halo-habitat and the Subarctic Front and the Subarctic Boundary in the North Pacific in winter and summer for sockeye and chum salmon, respectively. The relationship between Pacific salmon distribution and three

water column properties are listed in Table 2. In winter, the habitat with acceptable sea conditions for sockeye salmon in the western North Pacific was much narrower than that in the eastern North Pacific (Fig. 5a). The southern limit of sockeye salmon distribution in the western North Pacific corre-
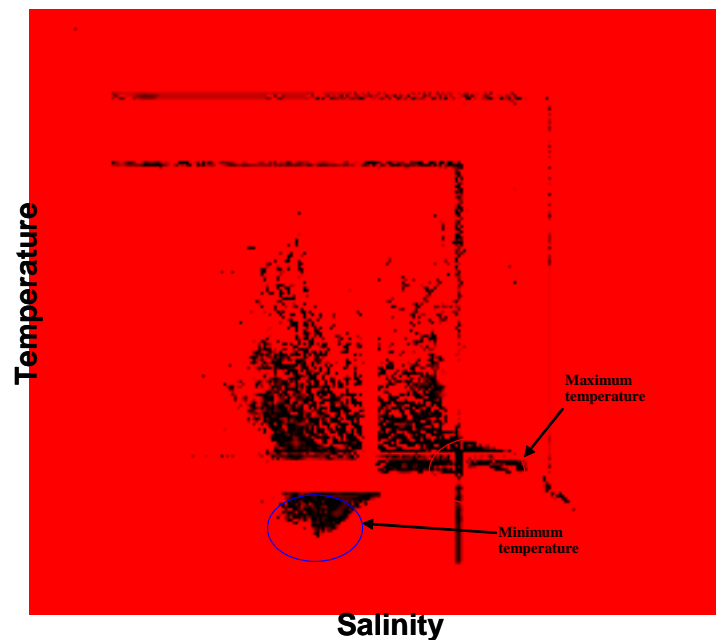
Fig. 3. The thermal and halo-limits for sockeye (red line), chum (green line), pink (purple line), coho (pale blue line), and chinook salmon (darker blue line) and the vertical profiles from 10 m to 1000 m at the observation points. Green dots indicate the Subarctic Current System, black dots indicate the Transition Domain, red dots indicate the Subtropical Current System, and pale blue dots indicate the Alaska Current System. Blue and red circles indicate the minimum and the maximum temperature, respectively.

Table 1. Thermal and halo-limits of salmon distribution.

Species	Upper thermal limit (°C)	Lower thermal limit (°C)	Upper halo-limit (PSU)
Sockeye	13.3	3.3	33.46
Chum	15.6	2.7	34.45
Pink	16.6	2.8	34.37
Coho	15.7	3.7	34.26
Chinook	13.4	-	33.95

Table 2. Relationship between the fronts in the North Pacific and salmon distribution. + is distribution, - is no distribution, and = is the boundary of the southern or northern distribution.

	Subarctic Front		Transition Domain		Subarctic Boundary	
Species	Winter	Summer	Winter	Summer	Winter	Summer
Sockeye	=	=	-	-	-	-
Chum	+	+	+	=	+	-
Pink	+	+	+	=	+	-
Coho	=	+	+	=	=	-
Chinook	+	=	+	-	=	-
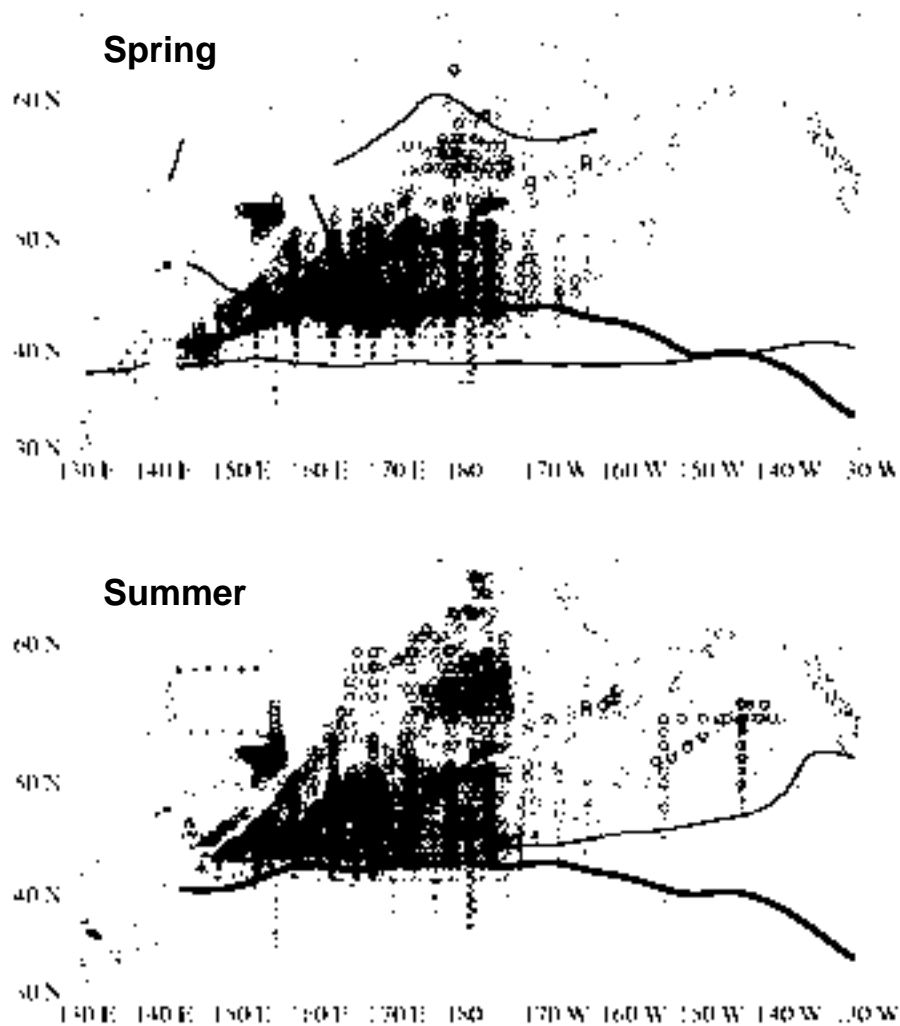
Fig. 4. Comparison between the thermal (thin line) and halo-limit (thick line) and the historical observations for sockeye salmon in spring and summer. X's indicate no catch and circles indicate catch.
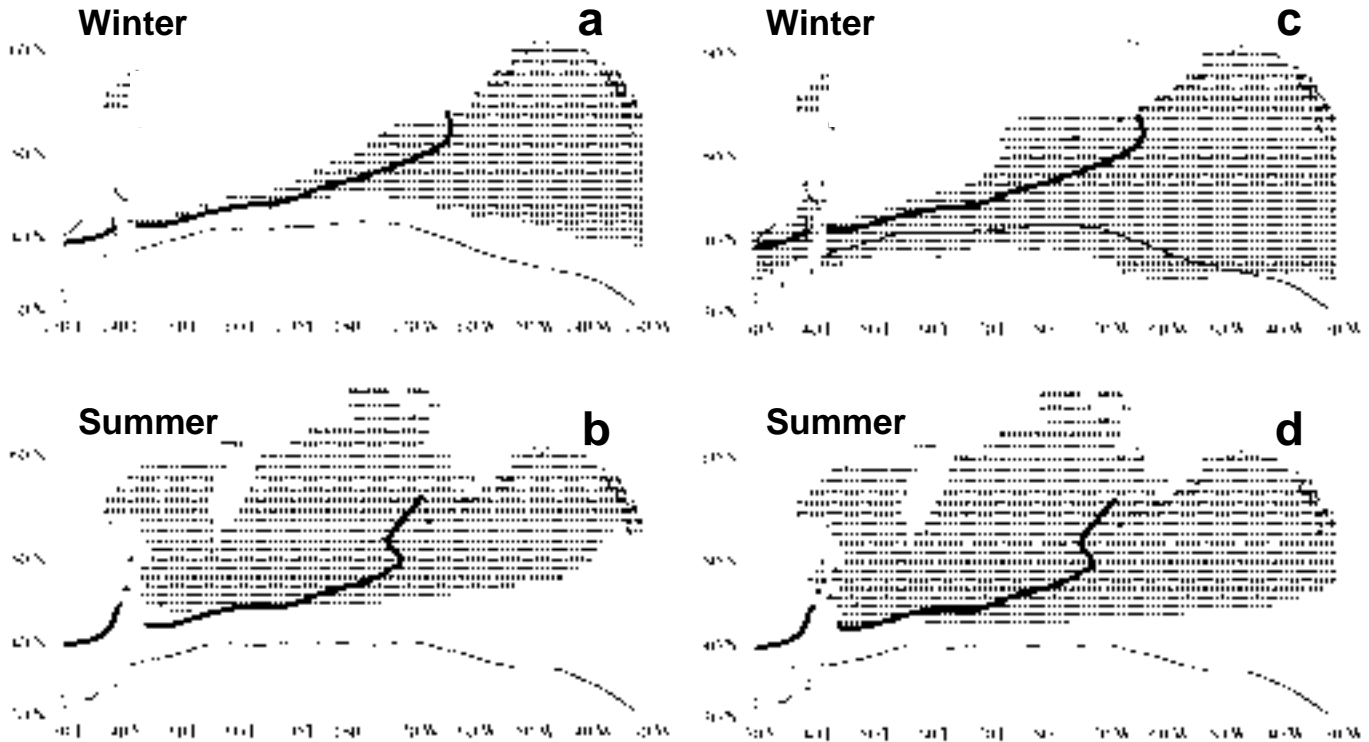
Fig. 5. Horizontal distributions of the thermal and halo-habitat (dots), the Subarctic Front (thick line) and the Subarctic Boundary (thin line). (a) winter, (b) summer for sockeye salmon; and (c) winter, (d) summer for chum salmon.

sponded to the Subarctic Front in both winter and summer (Fig. 5a,b). In summer, the southern limit of sockeye salmon distribution was located between 45°N to 50°N in the North Pacific and at 54°N near the coast of Alaska (Fig. 5b). In winter, the southern limit of chum and pink salmon distribution extended over the Subarctic Boundary in the North Pacific (Fig. 5c, Fig. 6a). The northern limit was located north of the Aleutian Islands. The southern limit of their distributions was located in the Transition Domain in summer (Fig. 5d, Fig. 6b). The southern limit of coho salmon distribution was located at the Subarctic Boundary, and the northern limit was located at the Subarctic Front in winter (Fig. 6c). Thus, the acceptable thermal and halo-habitats for coho salmon correspond to the Transition Domain. The southern limit of coho salmon distribution was located in the Transition Domain in summer, similar to that of chum and pink salmon (Fig. 6d). The southern limit of chinook salmon distribution in winter was located at the Subarctic Boundary. It was located at the Subarctic Front in summer.

Figure 7 shows the seasonal changes in the habitat of sockeye salmon. In winter and spring in the western North Pacific, the southern limit of distribution was dependent on the halo-limit. In the eastern North Pacific, the southern limit was dependent on the thermal limit during all seasons. By contrast, in summer, the thermal limit is similar to the southern limit of distribution in the North Pacific. The results for

sockeye salmon were similar to those for chum, pink, and coho salmon. Thus, the halo-limit during winter and spring was more important in determining the southern limit of Pacific salmon distribution rather than the thermal limit in the western North Pacific. If we examine the thermal limit of salmon distribution in the western North Pacific using only water temperature and fishing data collected in winter and spring, the calculated thermal limit will be the apparent limitation for salmon.

Areas of acceptable thermal and halo-habitat of salmon in winter and summer are listed in Table 3. The range of areas of thermal and halo-habitat for chum salmon in winter was wider than those for the other species. The range of areas of thermal and halo-habitat for sockeye salmon was the narrowest compared to other species in both winter and summer. In summer, areas of thermal and halo-habitat for pink salmon were wider than those for other species. The areas of thermal and halo-habitat for sockeye and coho salmon increase in summer. On the other hand, the areas of thermal and halo-habitat for chum and pink salmon decrease in summer because the southern limit of chum and pink salmon distribution shifts northward by about 10°N in the eastern North Pacific.

We examined the seasonal and regional changes in temperature at the southern limit of sockeye salmon distribution at 160ºE (squares), 180º (triangles) and 150ºW (circles)
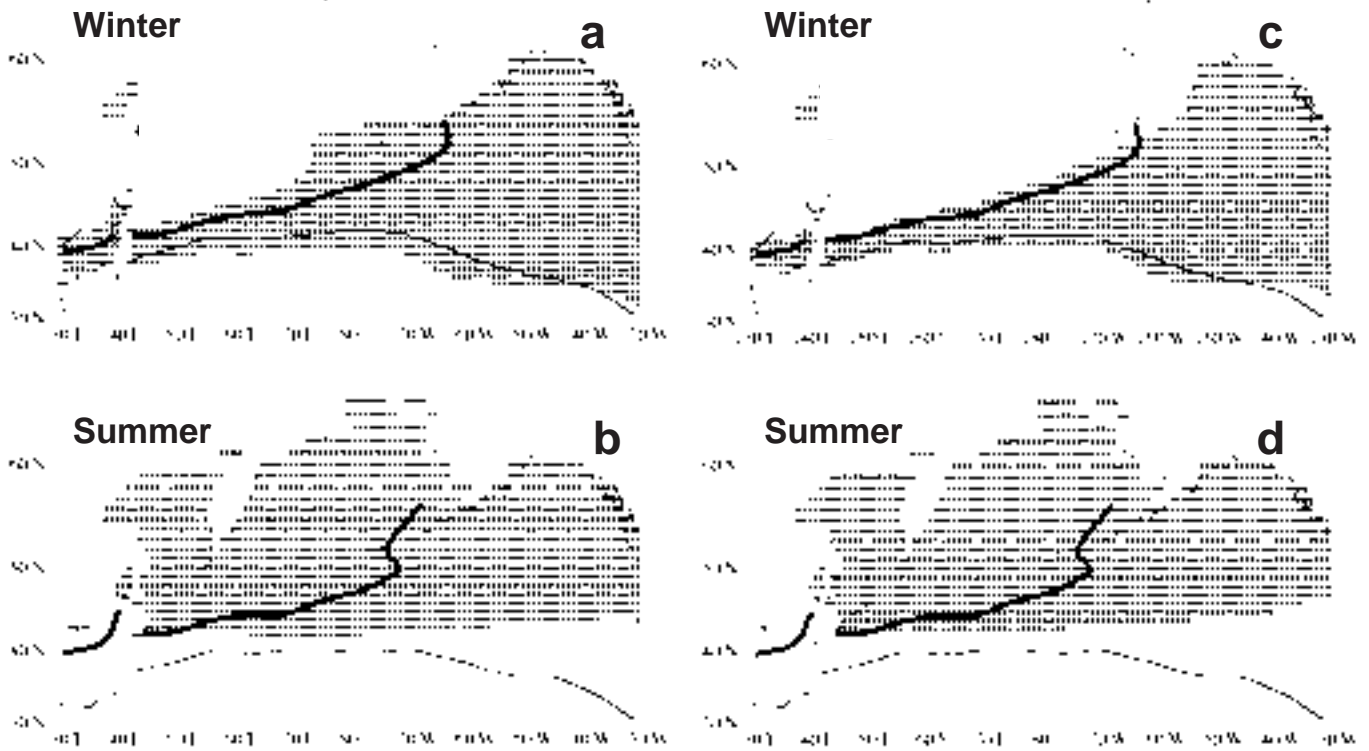
Fig. 6. Same plot as in Fig. 5 but in (a) winter, (b) summer for pink salmon; and (c) winter, (d) summer for coho salmon.
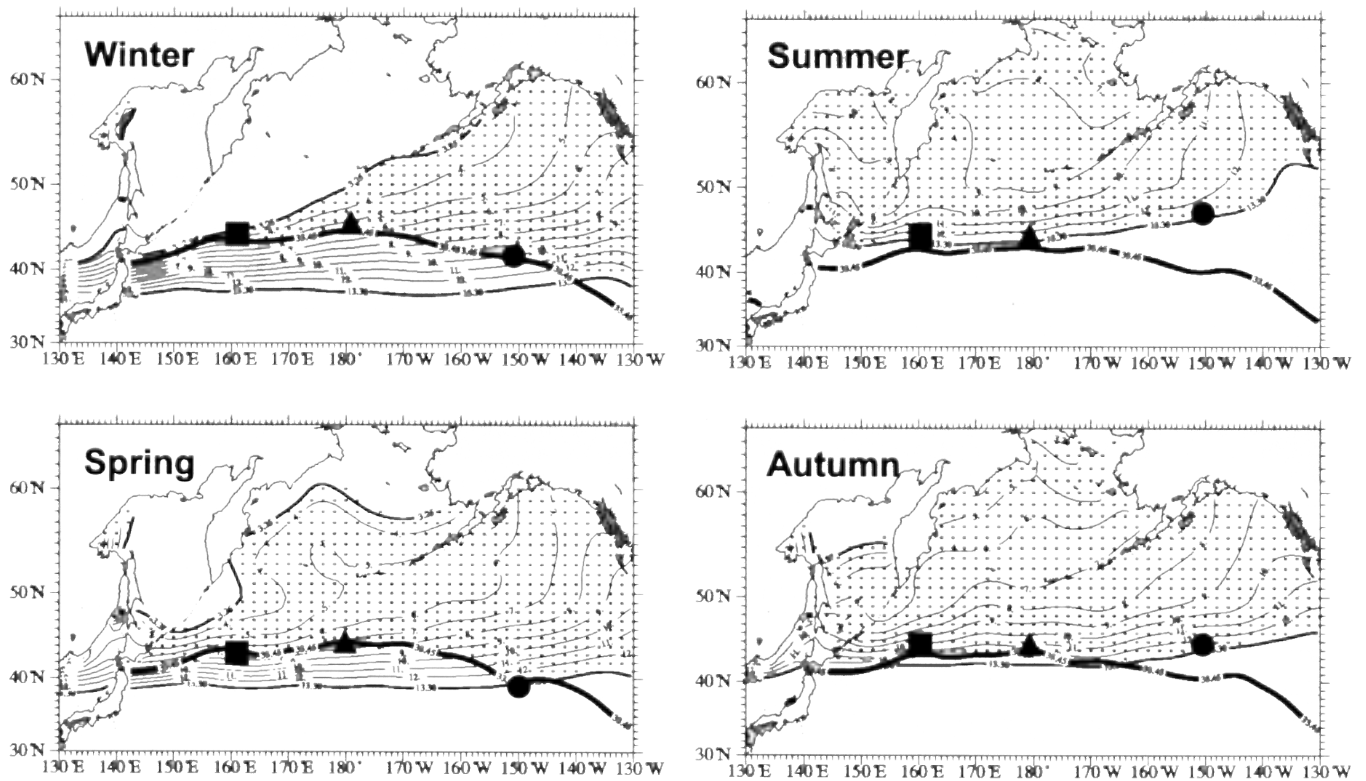
Fig. 7. Seasonal changes in the thermal (thin line) and halo-limits (thick line) for sockeye salmon. Dots indicate the thermal and halo-habitat. Solid squares (160ºE), triangles (180º) and circles (150ºW) indicate the locations where the seasonal changes in temperature at the southern limit were investigated. Contour lines indicate sea surface temperature.

Table 3. Areas of acceptable thermal and halo-habitat of salmon in winter and summer (x10^{7} km[2]). * In the case of climate warming.

Species	Winter		Summer	
Sockeye salmon	0.61	*0.83	0.87	*0.70
Chum salmon	1.24	*1.41	1.06	*0.95
Pink salmon	1.21	*1.47	1.14	*1.03
Coho salmon	0.99	*1.25	1.07	*0.96
Chinook salmon	-		-	
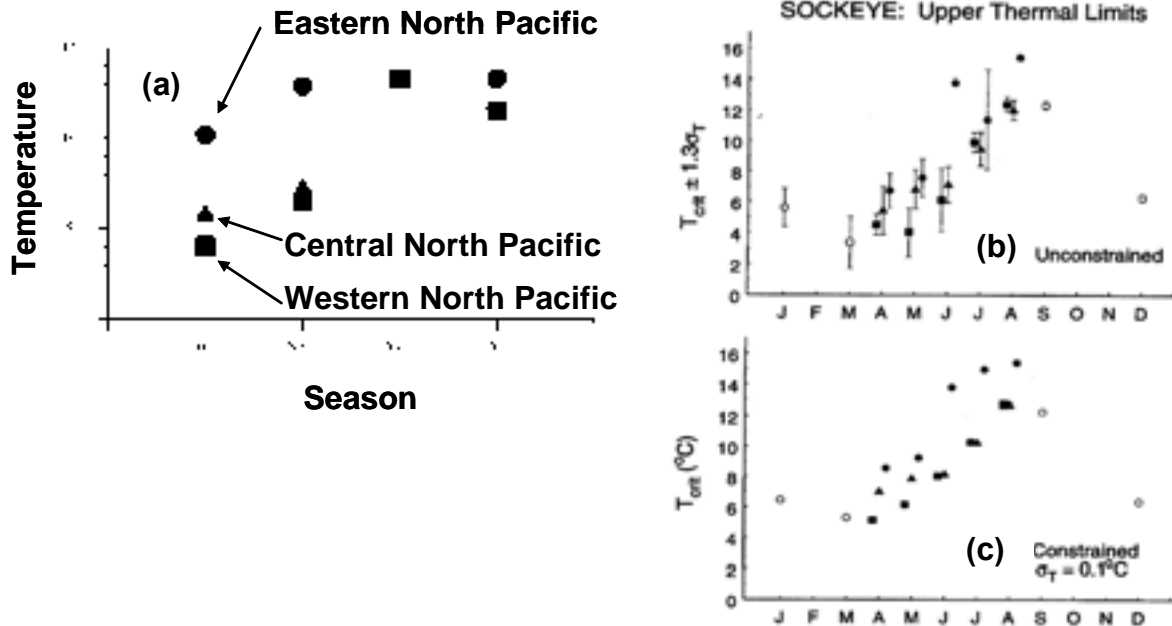
Fig. 8. Seasonal changes in temperature at the southern limit of sockeye salmon in the North Pacific. Estimated critical temperatures defining the southern limit of sockeye distribution, (a) This study and estimated critical temperatures defining the southern limit of sockeye distribution, Tcrit, in different months; (b) unconstrained, and (c) constrained (from Welch et al. 1999).

(see Fig. 7). The temperatures at the southern limit in the eastern North Pacific were higher than those in the western and the central North Pacific (Fig. 8a). The temperatures at the southern limit in winter were lower than those in summer. It is shown that the temperatures at the southern limit of salmon distribution varies seasonally and regionally.

Because the distribution of salmon is decided by not only horizontal limitations but also vertical limitations in sea conditions, the horizontal distributions of the depth (m) of acceptable thermal and halo-habitat for sockeye salmon in the North Pacific during the summer were examined. The depths of the thermal and halo-habitat for sockeye salmon in the Subarctic Current System were shallower than those in the central and eastern North Pacific (Fig. 9). By contrast, the depths of habitat were < 40 m in the eastern Bering Sea shelf and the Okhotsk Sea. The vertical distribution was limited by the upper halo-limit in the central and eastern North Pacific and by lower thermal limits in the western North Pacific and the Bering Sea.

DISCUSSION

Our study considered catch, while Welch et al. (1995) used CPUE to assess thermal limits. The thermal limits for salmon defined in this study were higher than those found by Welch et al. (1995). However, the trend in the upper thermal limits by species was similar to the temperatures at the southern limit of salmon distribution found by Welch et al. (1995): 10.4°C for chum and pink salmon, 9.4°C for coho salmon, and 8.9°C for sockeye salmon. In this study, we found that not only the thermal barriers but also the halo-barriers form an effective limit to salmon distribution in the North Pacific. If salmon remain in waters within the range of thermal and halo-limits, salmon will be distributed according to their preferred temperature or preferred food habitat. Welch et al. (1995) suggested that when food is limited, salmon move to an environmental temperature that will yield maximum growth. As a result, the temperature at the southern limit of salmon varies seasonally and regionally as shown in Fig. 8b, c (Welch et al. 1999). Our results as shown in Fig. 8a are similar to those of Welch et al. (1999). However, the temperature at the southern limit

Fig. 9. Horizontal distributions of the depth (m) of the acceptable thermal and halo-habitat for sockeye salmon in the North Pacific during the summer. Thick lines indicate the upper thermal limit; thin contour lines indicate depth. Shaded areas indicate that the vertical distribution of sockeye salmon was limited by the upper halo-limit. The white area indicates that the vertical distribution was limited by the lower thermal limit.

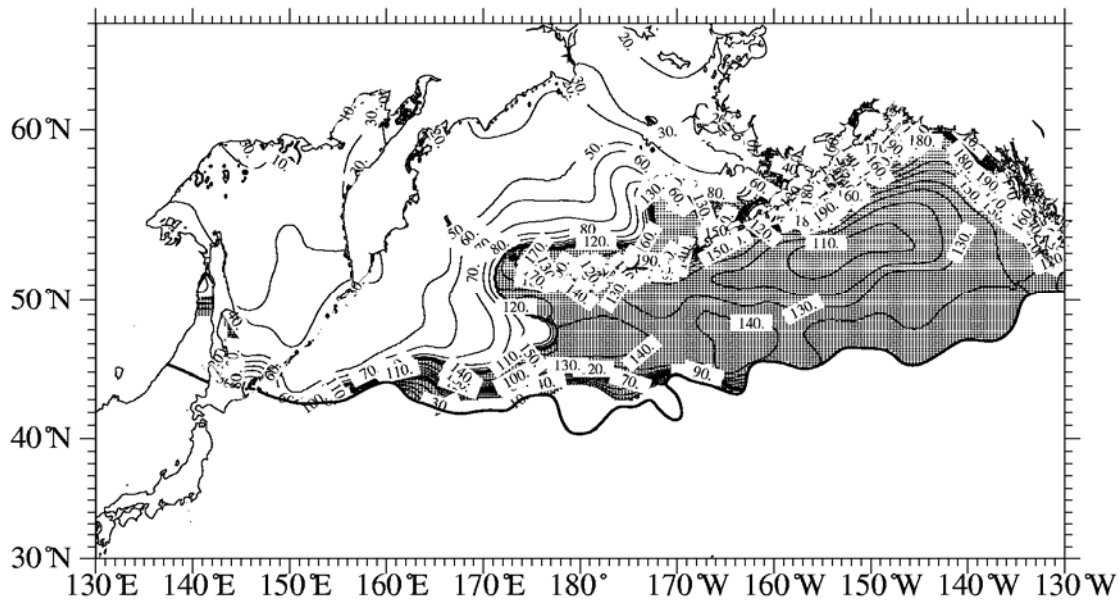of salmon distribution found by Welch et al. (1999) does not correspond with the detected upper thermal limit in this study. Thus, we note that the halo-limit results in seasonal and regional changes in temperature at the southern limit of salmon distribution. However, it is not clear how salinity affects salmon distribution. It has been suggested that salinity directly influences the metabolism of salmon through their osmotic pressure, and that the limit of food habitat for salmon may be seen as the upper halo-limit. The location of salinity fronts in the North Pacific often corresponds to the upper halo-limit. Studies on the relationships between salinity and metabolism and between salinity and food habitat of salmon will be needed in the future.

The limit of vertical salmon distribution is dependent on the lower thermal limit rather than the upper halo-limit in the Subarctic Current System, the western North Pacific and the Bering Sea (Fig. 9), because vertical changes in salinity are smaller than vertical changes in temperature over the range of thermal and halo-habitats. The characteristic water mass in the Subarctic Current System has minimum temperatures (blue circle in Fig. 3) at a depth of about 150 m and maximum temperatures (red circle in Fig. 3) at a depth of about 250 m. The minimum temperature is the result of cooling of the mixed layer in winter. The maximum temperature is about 1°C higher than the minimum temperature. Because the minimum temperature is < 2°C, and the salinity is about 33.0 to 33.25 psu, the minimum temperature is lower than the lower thermal limit for sockeye, chum, pink and coho salmon (Fig. 3). This suggests that sockeye, pink and coho salmon do not remain in the layer with the minimum temperature for

long periods of time or dive into this layer. Although chum salmon dive into minimum temperature water, they have a high frequency of movement between the sea surface and the minimum temperature layer so that their body temperature does not decrease significantly (Azumaya and Ishida, 2005). The coldest layer limits the vertical distribution of sockeye, chum, pink and coho salmon, such that the depths of habitat in the Subarctic Current System are shallower than those in the central and eastern North Pacific (Fig. 9). By contrast, because the depths of thermal and halo-habitat are < 40 m in the eastern Bering Sea shelf and the Okhotsk Sea, these areas are unsuitable as salmon habitat. The lower thermal limit for chinook salmon was < 1.6°C, which was lower than the minimum temperatures in the Bering Sea and the North Pacific. Thus, there is a possibility that chinook salmon remain in the mixed layer at relatively low temperatures in winter in the Bering Sea and the North Pacific. Ishida et al. (1999) showed that chinook salmon are distributed in the Bering Sea in February.

We speculated about the influence of climate warming on the salmon distribution using thermal and halo-limit. Table 3 shows the area of the acceptable habitat for salmon when the mean water temperature increases by 1.5°C and salinity decreases by 0.2 psu in the North Pacific as a result of homogeneous climate warming. These theoretical climate conditions assume that atmospheric CO_2 concentrations increase by 1% per year over a period of 70 years. In summer, the upper thermal limit shifts northward. Thus, the area of salmon distribution decreases by 13% compared to current values. In particular, the decrease in area in the east-

ern North Pacific is quite remarkable. However, in winter, the lower thermal limit shifts northward, so that the area of salmon distribution increases by 19% compared to today.

In conclusion, we reanalyzed the relationship between salmon distribution and water temperature and salinity in the North Pacific Ocean. The thermal limit and the upper halo-limit of salmon distributions were found. The range of the thermal and halo-limits for pink salmon was wider than that for other species. The range for sockeye salmon was narrower than that for other species. Because the upper halo-limit for sockeye salmon was the lowest of all species, sockeye salmon appeared to be distributed in relatively low temperature water. The occurrence of the halo-limit results in seasonal and regional changes in temperature at the southern limit of salmon distribution.

ACKNOWLEDGEMENTS

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Spatial Distribution and Age Composition of Chum Salmon in the Western Bering Sea in 2002 and 2003

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Abstract: This work was based on data from three epipelagic trawl salmon surveys of TINRO-Centre in the western Bering Sea in July–August 2002 and July–October 2003. We examined spatial distribution, age structure, and body size of chum salmon (*Oncorhynchus keta*). In fall (September and October) 2002–2003, the abundance of immature and maturing chum salmon was highest in the western Aleutian Basin and vicinity. In summer (July and August) 2003, the spatial distribution of chum salmon was more aggregated. Juvenile chum salmon were concentrated in the shelf break areas during the fall after leaving the inshore regions. During the summer and fall immature chum salmon (mostly age 0.1 and 0.2) dominated in the deepwater and shelf break areas. Maturing chum salmon (age 0.3 and 0.4) were prevalent in the shelf areas during summer, while they were almost absent in the western Bering Sea during fall.

Keywords: chum salmon, spatial distribution, age structure, western Bering Sea

INTRODUCTION

Chum salmon (*Oncorhynchus keta*) is the most widely distributed and the second most abundant species of Pacific salmon. They are distributed in Asia from Korea to the Arctic coast of Russia and in North America from California to the Beaufort Sea. They are also an important part of the inshore fisheries. During 1971–2005 the Russian catches of chum salmon ranged from 8.4 thousand tons to 32.4 thousand tons.

The marine life history of chum salmon has received considerable attention in recent decades. The first investigations were conducted in the middle of the 20th century (Ricker 1964; Smirnov 1975; Birman 1985). At present, there are many studies that address Pacific salmon ecology, including the comprehensive papers by Shuntov (1989), Salo (1991), Shuntov et al. (1993), Sobolevskyi et al. (1994), and Starovoitov (2003). In this paper, we present new data on the spatial distribution, age composition, and size structure of chum salmon in the western Bering Sea.

MATERIALS AND METHODS

This work is based on three midwater trawl surveys conducted by TINRO-Centre in the western Bering Sea from 2 September to 9 October 2002, from 17 July to 24 August 2003, and from 23 September to 25 October 2003 (Fig. 1). The vertical spread of the net was 31–41 m and the horizontal spread was 38–44 m, depending on towing speed. Trawls were conducted in the subsurface layer during both day and night. All trawls lasted one hour (except at one station) at an average ship speed of 4.6 kt.

The study area was divided into three primary regions: a shelf region (Anadyr Bay, < 150 m depth), a shelf break region (Olutorsky, Koryaksky and Navarinsky shelf breaks, 150–500 m depth) and a deepwater region (Komandor and western Aleutian basins, > 500 m depth) (Fig. 1). Catches of chum salmon were counted, weighed and standardized to individuals per km^2. The average density was estimated for three primary regions as: $N = n/(S \cdot k)$, where N is chum salmon abundance per km^2, n is chum salmon abundance in the catch, S is trawled area in km^2 and k is the catchability coefficient (k = 0.3 for adult and 0.4 for juvenile chum salmon).

For each fish, fork length and body weight were measured, sex and stage of maturity were determined and a scale sample was taken. Scale samples were collected from chum salmon using the method described by Clutter and Whitesel (1956), Knudsen (1985), and Knudsen and Davis (1985). The number of scale samples was 1879 in fall 2002, 2,196 in summer 2003, and 1,531 in fall 2003. Chum salmon were categorized as juvenile (ocean age 0.0), immature (ocean age $\geq$ 0.1, fish will not spawn in this year) and maturing (fish will spawn in this year).

RESULTS AND DISCUSSION

Immature and maturing chum salmon densities in the deepwater and shelf regions were similar in fall 2002 and fall
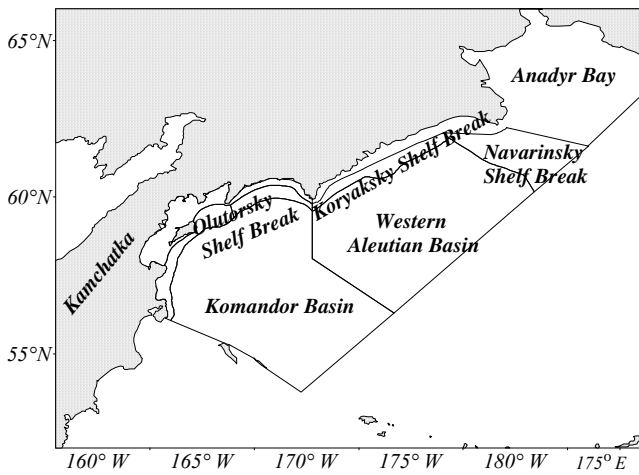
Fig. 1. Map of the study area in the western Bering Sea.

the Komandor and Aleutian basins (Fig. 4a, c); the percentage of maturing chum salmon was low. In summer, catches of maturing fish were higher, but they dominated only in the northern part of Anadyr Bay (Fig. 4b). Despite this dominance, chum salmon density in this region was low (Table 1). Thus, most of chum salmon catches in summer 2003 consisted of immature fish. There was likely more intensive migration of immature chum salmon to the western Bering Sea in summer 2003. In summer 2003 maturing chum salmon dominated in shelf and shelf break areas (Fig 4b). Their abundance ranged from 34 to 306 ind/km². Maturing chum salmon density was lower in the deepwater regions. In fall 2002 maturing chum salmon were observed at almost every location in the survey area. The highest density was in the Aleutian Basin (156 ind/km²; Fig. 4b). In contrast, in fall 2003 maturing chum salmon abundance was low, and they occurred only in the deepwater regions (Fig. 4c).

The highest concentrations of juvenile chum salmon were confined mainly to the Olutorsky region, the northwestern Komandor Basin and Anadyr Bay (Fig. 3). In the deepwater regions of the Bering Sea the catches of juveniles were low. Consequently, they concentrate in the continental shelf break regions during the fall after leaving the inshore regions. A relationship between juvenile spatial distribution and surface temperature was observed. It is assumed that chum salmon avoid sea temperatures < 5–6°C (Azumaya et al. 2005). In 2002, juvenile chum salmon were widely distributed in Anadyr Bay. In 2003, however, they were caught only in southeastern Anadyr Bay (Fig. 3).

Juvenile chum salmon moved further from shore as they grew. As a result, their average length in the inshore regions was less than in offshore regions (Fig. 3). The mean fork length of juvenile chum salmon was also different in the southwestern regions compared to northeastern regions, mainly as a result of the differences in times of trawl surveys. The survey began in September in the southwestern Bering Sea and was completed in October in the northwestern Bering Sea.

The age composition of chum salmon was different

2003 (Table 1). In the shelf break region immature and maturing chum salmon were more numerous in 2002. Juvenile chum salmon were more abundant in fall 2003 compared to fall 2002, excluding the shelf region. In 2003, fish concentrated in deep water and shelf break zones. In 2002, they were most abundant on the shelf. This difference may be explained by the later dates of the survey in fall 2003. Juvenile chum salmon tended to move from the shelf to deepwater areas after downstream migration.

In summer 2003, immature and maturing chum salmon concentrated in the deepwater and shelf break regions (Table 1). Juvenile salmon were absent from the trawl catches, because they foraged in inshore regions outside of the study area. The density of immature and maturing chum salmon was greater in the summer than in the fall. Their abundance was the highest in the deepwater regions in fall and summer 2002–2003 and on the shelf break in summer 2003 (Table 1, Fig. 2). Within the deepwater zone they were more aggregated in the Aleutian Basin.

In fall, immature chum salmon dominate, especially in

Table 1. Density (ind/km²) of chum salmon in the different regions of the western Bering Sea. Imm/mat = immature and maturing fish; N = number of stations.

		Fall 2002		Fall 2003		Summer 2003	Fall 2002–2003	
		Juvenile	Imm/mat	Juvenile	Imm/mat	Imm/mat	Juvenile	Imm/mat
	average	53	1,000	208	982	1,737	130	991
Deep water	range	0–1,428	23–2,911	0–4,473	0–4,749	105–144,404	0–4473	0–4,749
	N	45		44		42	89	
	average	45	395	111	81	2034	78	238
Shelf break	range	0–203	0–3,019	0–520	0–254	87–8,714	0–520	0–3,019
	N	10		10		11	20	
	average	101	8	3	4	458	50	6
Shelf	range	0–1,003	0–58	0–39	0–37	0–4,201	0–1,003	0–58
	N	18		19		18	37	

190
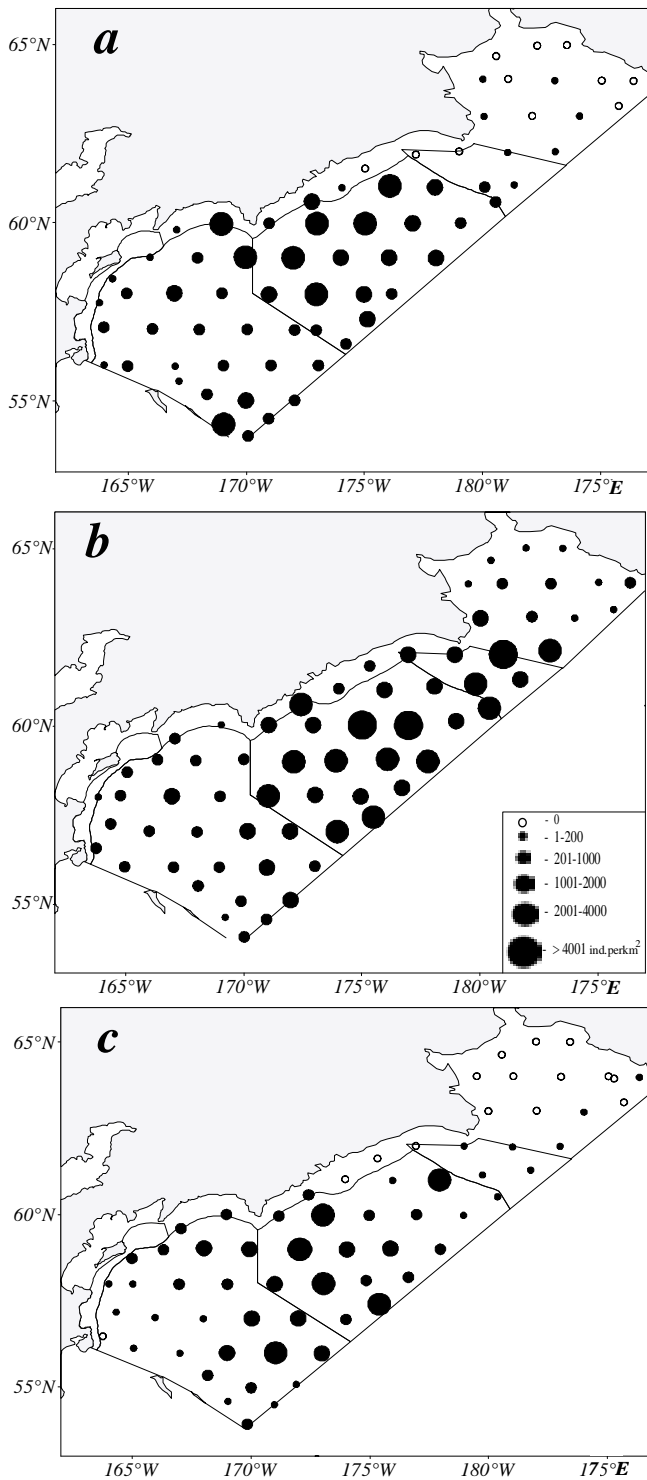
Fig. 2. Density distribution of trawl catches of immature and maturing chum salmon in fall 2002 (a), summer 2003 (b), and fall 2003 (c).

Fig. 3. Surface temperatures (lines), and density distribution (contour) and average fork length (triangles) of juvenile chum salmon in the western Bering Sea in fall 2002 (a) and 2003 (b).

Basin, and the Aleutian and Koryaksky shelf breaks. Their percentage was < 13% in the fall of 2002, while it was higher and fluctuated from 13% (Koryaksky shelf break) to 42% (Aleutian Basin) in the fall of 2003.

In the summer of 2003, the predominant age group in the Aleutian and Komandor basins and the Koryaksky shelf break was 0.1 (44%, 59%, and 61%, respectively). Age 0.2 and 0.3 fish were found in the shelf regions. Immature chum salmon (mostly age 0.1 and 0.2) dominated in the deepwater and shelf break areas especially in the Komandor and Aleutian basins during the summer and fall. Maturing chum salmon (age 0.3 and 0.4) dominated in the shelf and shelf break areas during summer, but maturing fish were nearly absent in the western Bering Sea during fall. Similar distributions were observed earlier (Sobolevskyi et al. 1994; Starovoitov 2003; Sviridov et al. 2004).

among regions, seasons and years. In fall, age 0.2 fish dominated in the deepwater zone. Their percentage varied from 45 to 79% in different regions in 2002 and from 23 to 88% in 2003. Juvenile chum salmon foraged in the Komandor
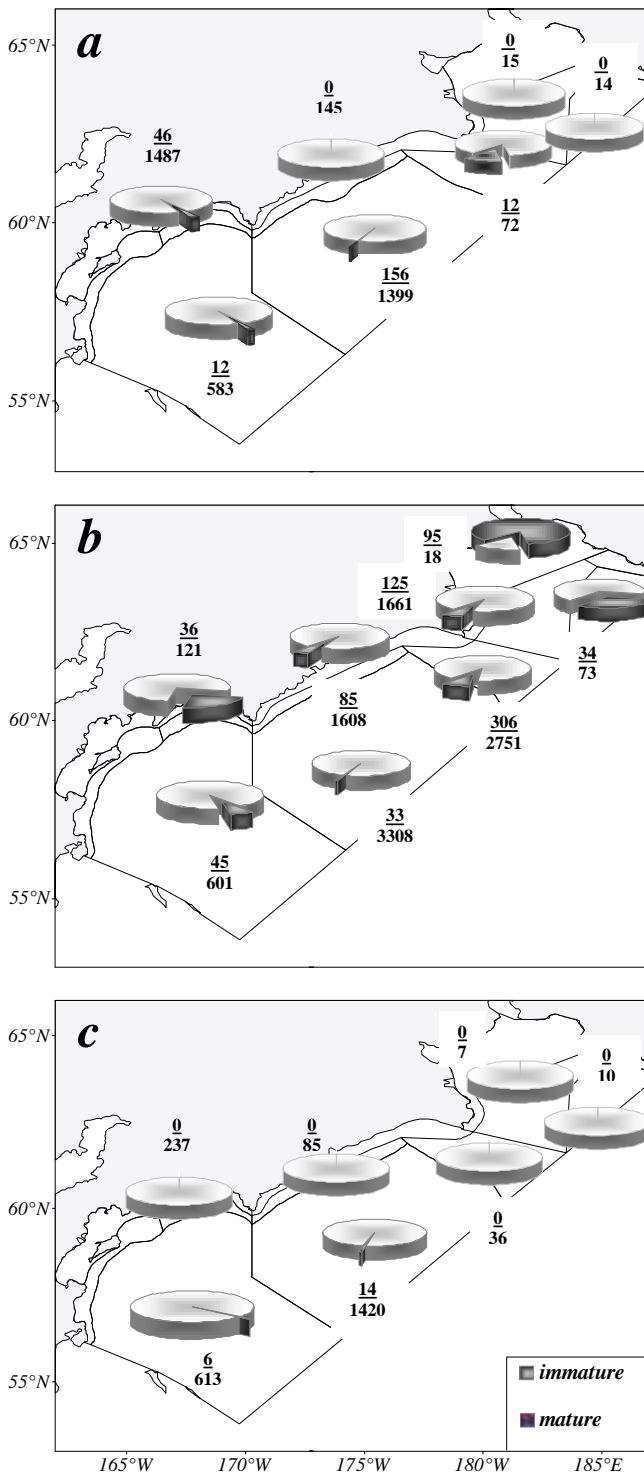
Fig. 4. Percent and average density (ind/km²) of maturing (nomina-
tor) and immature (denominator) chum salmon in the western Bering
Sea in fall 2002 (a), summer 2003 (b) and fall 2003 (c).

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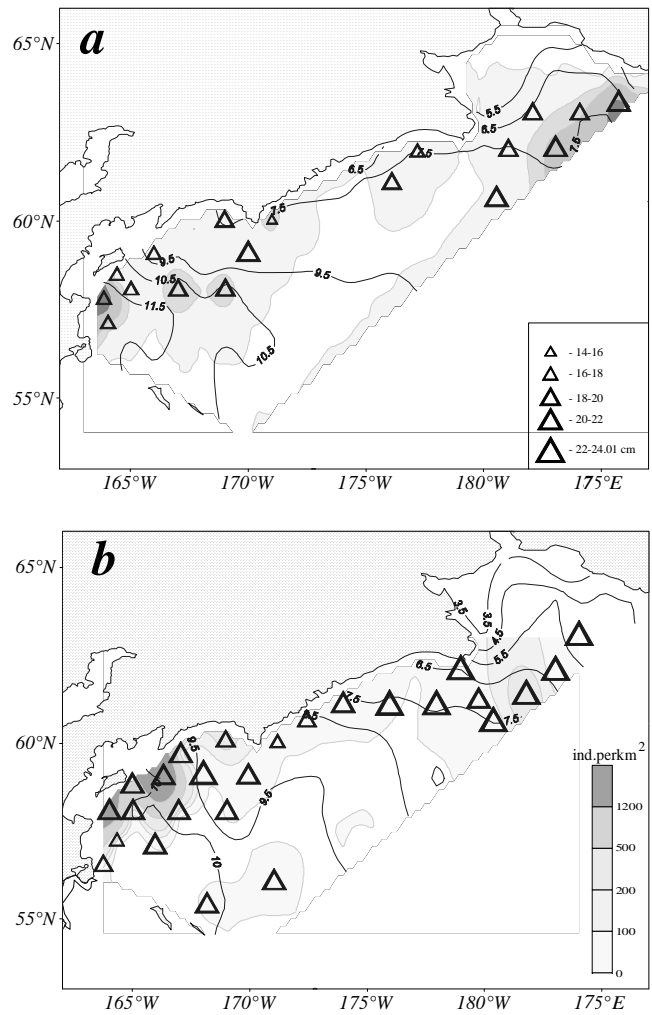
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Spatio-Temporal Variation in Vertical Distributions of Pacific Salmon in the Ocean

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Abstract: The vertical distribution of Pacific salmon (*Oncorhynchus* spp.) is of interest to biologists and the fishing industry. An understanding of the normal vertical distribution and movement of salmon facilitates better management of both directed and non-salmon fisheries and better evaluation of research data. Salmon vertical distribution can vary spatially in relation to distance from shore, depth of the water column, and by ocean region, and temporally by life-history stage, season, time of day, and ocean conditions. In coastal waters, juvenile salmon were usually less than 15 m from the surface. In offshore waters, salmon were usually within the top 40 to 60 m, above the thermocline, but occasionally were found from 80 to 120 m. They usually were near the surface at night, and moved vertically during the day. Sockeye salmon displayed the shallowest vertical distribution, followed by pink, coho, chum, and Chinook salmon. There are limited data for winter, but vertical distributions may not change substantially from summer in offshore waters, while it may shift in some species in coastal and shelf areas. There is a need for more long-term data, throughout the marine residency of individual fish.

Keywords: Pacific salmon, vertical distribution, depth, diel behavior, data storage tags

INTRODUCTION

The depths to which Pacific salmon (*Oncorhynchus* spp.) dive has long been of interest to biologists and the fishing industry. It is important to understand the normal vertical distribution and movement of salmon for a number of reasons. Non-salmon fisheries may be better managed to avoid salmon by-catch if salmon vertical distribution and behavior are known. Also, the effect of changes in ocean and climate conditions on salmon distribution and abundance may be more accurately assessed. Salmon surveys may be better planned and survey data can be better evaluated if vertical distribution information is used when considering time of sampling, season, depth of gear, region surveyed, and age and species of salmon.

Salmon vertical distribution may vary spatially for a number of reasons, including distance from shore, depth of the water column, and ocean region. It may also vary temporally as a function of life-history stage, season, time of day, and ocean conditions.

Fisheries scientists have used a number of different methods and equipment to explore the depths at which salmon may be found. These include gillnets (Manzer 1964; Machidori 1966; French et al. 1971; Straty 1974; Pearcy and Fisher 1988), longlines (Godfrey et al. 1975), trawls (Ueno 1992, 1994; Erickson and Pikitch 1994; Radchenko and Glebov 1997, 1998), trolling (Beacham 1986; Orsi and Wertheimer 1995), hydroacoustics (Nero and Huster 1996; Sakai et al. 1997), ultrasonic and radio tags (Quinn 1988; Quinn et al. 1989, Ruggerone et al. 1990; Ogura and Ishida 1992, 1995; Ogura 1999), and archival data tags (Wada and Ueno 1999; Tanaka et al. 2000, 2001; Walker et al. 2000; Ishida et al. 2001; Murphy and Heard 2001, 2002; Azumaya and Ishida 2005; Tanaka et al. 2005). There are limitations for all these types of gear that may lead to biases in the results.

Here we present new data from trawl surveys, bycatches and data storage tags, and review and compare previously published information on salmon swimming depths.

MATERIALS AND METHODS

24-Hour Trawl Observations

In 2003 and 2004, scientists aboard the Russian research

vessel *TINRO* conducted trawls throughout 24-h periods in August and September in the Aleutian Basin of the Bering Sea at 58°N, 172°E. Trawl surveys were conducted using a midwater rope trawl (40 m vertical opening; 30 m long; trawl opening perimeter 396 m; headrope length 80 m; four bridles 100–120 m long; warp lengths 245–280 m) towed for one hour. In 2004, over a 14-day period the trawl was set every four hours such that the headrope was at nine different levels on successive hauls: 0, 40, 80, 120, 160, 200, 350, 500, and 750 m. Depths were verified by acoustic readings. Each stratum was sampled seven times (Glebov et al. 2005). In 2003 the sampling was conducted at 0, 30 and 60 m over three days. The number of each species caught at each depth was counted and expanded to an index of abundance (number per cubic kilometer) using a formula based on catch of a species, weight of that species in the catch, size of the opening of the trawl, trawl speed and duration, and a fishing efficiency coefficient (0.3 for salmon longer than 30 cm, 0.4 for those shorter than 30 cm) (Sviridov et al. 2003).

Trawl Bycatch Data Analysis

A data set of information on Chinook salmon (*O. tshawytscha*) caught incidentally in eastern Bering Sea trawl fisheries from 1997 to 2000 was examined. Fishing depth (as determined by fishermen using various instrumentation and reported in logbooks) was used as the depth at which Chinook occurred. Data on depth of capture were stratified into month and ocean age (number of winters spent at sea) of the fish. Age and depth information were available for 5,246 fish. Most of the data were collected in January–February (48%) and September–October (45%).

Information from Data Storage Tags

Data from several types of data storage tags (DSTs) were summarized. Tags recording pressure (converted to depth data) were deployed from research vessels from 1999 to 2005 and recovered in those years. Tags included models RL-41 and RL-42, manufactured by Conservation Devices, Inc., and refinements of these tags manufactured by Lotek Marine Technologies, models LTD_1100-300 and LTD_1100-500. DST CTD tags manufactured by StarOddi were also used. CDI and Lotek tags had depth resolutions of 1 or 2 m. StarOddi tags had a resolution of 0.15 m.

Fish were captured for tagging by research longline, hook-and-line, and trawl on Japanese and U.S. research vessels. Tags were attached to fish just anterior to the dorsal fin using two nickel pins, with labeled disk tags placed on the pins on the other side of the fish. DST CTD tags were attached in the same location and with the same method, but were affixed with stainless steel wire, with a small oval plastic plate on the opposite side of the fish.

In the initial period after tagging, salmon sometimes remained near the surface for several days to more than a week, probably due to trauma from tagging (Walker et al. 2000). Data from this period were considered abnormal and were excluded. As chum salmon (*O. keta*) approach coastal areas on their homeward migration, they sometimes dive to great depths (> 200 m; Ueno 1992, 1994; Wada and Ueno 1999; Azumaya and Ishida 2005). These data were included in calculations of depth distributions.

Day and night periods were estimated from times of sunrise and sunset at release and recovery locations on the days a fish was tagged and recovered. A linear interpolation
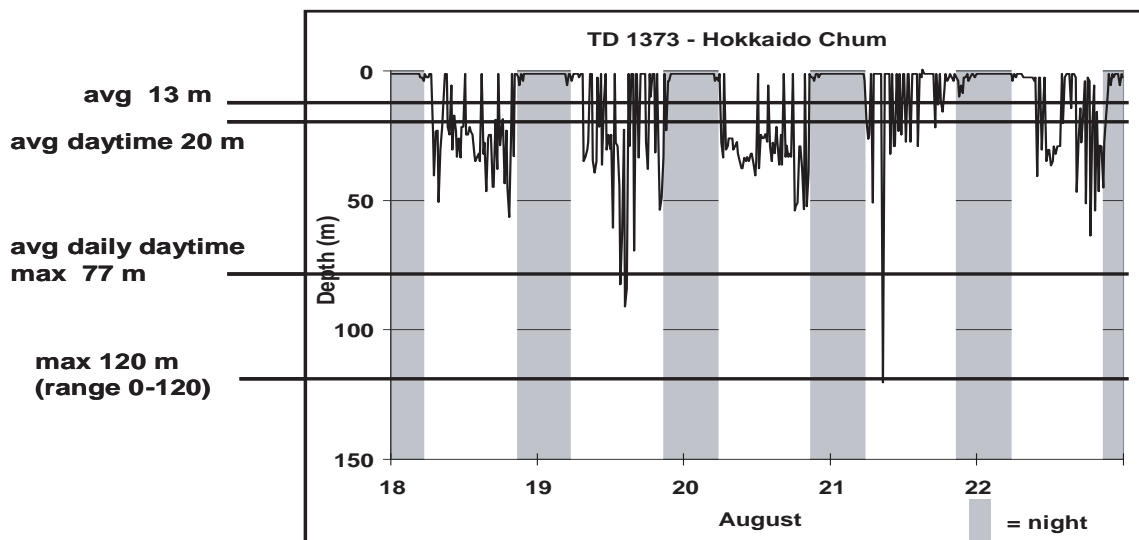

Fig. 1. Example of differences in calculations of average (daily) depth, average daytime depth, average daily maximum depth, and maximum depth. Data from a 5-day period recorded on temperature-depth data tag TD 1373 during homeward migration of a chum salmon returning to Hokkaido, Japan, from the Bering Sea in 2002.

was made between these endpoint values, producing a 'sunrise' and 'sunset' value at each data point recorded. Each data point also had an actual time of day recorded by the tag. The actual times were tested against the estimated times of sunrise and sunset at that point, and if the actual time was between the estimated sunrise and sunset, that point was characterized as a daytime value. Because day and night characterizations were estimated, fits with actual local diurnal cycles were not likely to be completely accurate. This would lead to some daytime data points being incorrectly characterized as nighttime, and vice versa. Thus the day/night differences we report are most likely smaller than they actually were.

In addition to calculating average depths, average 'maximum' depths were also calculated. This entailed finding the maximum depth recorded for each day (24 h), daylight, or nighttime period, and averaging these maximum depths (Fig. 1). Average daily minimum depths were also calculated.

RESULTS

24-Hour Trawl Experiments

In 2004, only immature (as assessed by gonad weight-body weight indices) chum salmon were taken in appreciable numbers (2.4% of immature chum captured) at depths other than 0 to 40 m (Table 1). Other species and maturity groups (maturing chum, juvenile (as estimated from body length) and maturing coho, *O. kisutch*) were taken only in the 0–40 m layer, except for a few immature sockeye (*O. nerka*) (40 to 80 m in the afternoon) and immature Chinook salmon (120 to 160 m at noon). It is likely that the rare catches of immature chum salmon at deep strata were artificial and were taken at shallower depth during the process of setting and retrieving the trawl. The decrease of chum salmon CPUE in the 0–40 m layer in evening, with no simultaneous significant increase of CPUE in deeper water layers, is likely attributable to migration within the upper 40 m to a level very near

Table 1. Estimated abundance of salmon (fish/cubic km) in diurnal trawl experiments at 6 depth strata within the Aleutian Basin, western Bering Sea (58°N, 172°E) from 23 August to 5 September, 2004. Im = immature; Mat = maturing; Juv = juvenile.

Depth (m)	Species	Morning	Noon	Afternoon	Evening	Midnight	Late night
0–40	Im chum	46,638	49,387	72,759	17,273	44,902	42,494
	Im sockeye	12,823	17,261	25,346	1,678	13,764	11,414
	Im Chinook	798	1,307	1,059	987	2,156	2,870
	Juv coho	66	0	91	219	110	189
	Mat chum	165	0	258	89	0	615
	Mat coho	91	0	0	83	0	0
40–80	Im chum	313	466	1,240	0	0	1,627
	Im sockeye	0	0.0	310	0	0	0
80–120	Im chum	0	2,295	0	0	0	0
	Im Chinook	0	156	0	0	0	0
350–390	Im chum	0	296	0	0	0	0
500–540	Im chum	281	0	0	0	0	0
750–790	Im chum	0	313	0	0	0	0

Table 2. Estimated abundance of salmon species (fish/cubic km) in diurnal trawl experiments within three depth strata within the Aleutian Basin, western Bering Sea (58°N, 172°E) during 8–10 September, 2003. Im = immature; Mat = maturing; Juv = juvenile. Times of day represent 6 sets of tows conducted 4 hours apart.

Depth (m)	Species	Morning	Noon	Afternoon	Evening	Midnight	Late night
0–30	Im chum	12,096	51,672	56,999	71,102	69,971	47,348
	Im sockeye	3,122	4,665	4,324	3,878	9,426	12,522
	Im Chinook	780	1,435	1,572	1,300	2,175	0
	Juv coho	0	0	294.8	141.4	544	0
	Mat chum	390	359	786	734	1,088	0
60–90	Im chum	303	1,827	2,768	1,204	156	293
	Im sockeye	0	609	0	301	0	293
	Im Chinook	303	0	308	0	0	0
90–120	Im sockeye	0	290	0	0	0	0

Table 3. Average depth in meters of bycatch of Chinook salmon in eastern Bering Sea trawl fisheries (1997–1999), tabulated into ocean age (winters spent at sea; all freshwater ages are combined, and represented by the dash preceding the period). Percentage of catch within 25-m depth intervals is also presented.

Ocean age (yrs)	January–February						September–October				
	-.1	-.2	-.3	-.4	-.5	All ages	-.1	-.2	-.3	-.4	All ages
N	39	279	1,317	798	82	2,515	368	1,455	497	20	2,340
Avg. depth (m)	58.1	107.8	65.9	51.2	47.7	65.2	80.8	78.1	69.6	63.0	76.6
25m depths	%										
0		0.7	1.9	2.5	1.2	1.9	0.0	0.0			
25	79.5	41.6	55.0	62.9	72.0	56.9	33.4	18.6	23.5	30.0	22.1
50	10.3	21.9	29.7	29.6	24.4	28.3	20.4	35.6	45.9	50.0	35.5
75		3.6	2.3	0.9		1.9	15.8	22.5	16.5	15.0	20.1
100		2.2	0.5			0.5	11.4	12.4	7.4		11.1
125	2.6	0.7	0.5	0.3		0.4	9.5	6.9	3.8	5.0	6.6
150			0.3	0.1		0.2	6.8	3.2	2.2		3.5
175		2.2	1.3	0.4		1.0	1.9	0.9	0.6		1.0
200	5.1	5.0	1.5	1.5		1.9	0.5				0.1
225		5.4	3.1	0.9	1.2	2.5					
250	2.6	9.7	2.6	0.4		2.6	0.3				0.0
275		6.8	1.3	0.6	1.2	1.7					
300		0.4	0.2			0.1					

the surface, where the trawl may not fish effectively.

In the September 2003 diurnal experiments, nearly all salmon (mature chum, juvenile coho, and immature chum, sockeye, and Chinook salmon) were taken in the 0 to 30 m layer (Table 2). Immature chum salmon were also taken between 30 and 60 m throughout the 24-hr period. A few (3.8% of sockeye caught) immature sockeye salmon were taken at depth intervals 30 to 60 m and 60 to 90 m, and a few (7.8%) immature Chinook salmon at 30 to 60 m. While the net opening was not closed during set and retrieval, for the great majority of the time the net fished at the targeted depth. While a few fish may have been caught during set or retrieval, the fact that almost all salmon were caught in the top (0–40 m) interval demonstrates that few fish are taken during ascent or descent to deeper depths.

Trawl Bycatch Data Analysis

Eastern Bering Sea groundfish trawl bycatch of Chinook salmon included more older fish in winter (87% ocean age -.3 and older) and more younger fish in summer–fall (78% ocean age -.1 and -.2). Over 90% were caught between 25 m and 175 m; less than 3% were deeper than 300 m. Chinook were slightly deeper in autumn (77 m average fishing depth in September–October, vs. 65 m January–February), and younger fish tended to be slightly deeper than older fish (Table 3).

Depth distribution showed a bimodal tendency in winter, with the bulk of fish at 25–75 m and a smaller peak at 200–300 m.

Although groundfish trawling was not conducted to catch salmon or carried out according to any systematic or experimental design, the large quantity of data provided by the fishery gives a good picture of Chinook vertical distribution during the fishery. Similar trawl data from the U.S. West coast yielded important information on Chinook depth distribution and seasonal changes (Erickson and Pikitch 1994). The insights on changes in age distribution and at what depths Chinook salmon are most likely to be found can provide valuable guidance to managers and fishermen.

Data Storage Tag Experiments

Depth data from a limited number of DSTs (n = 38) confirm that Chinook and chum salmon had the deepest vertical distributions. Average depths (Chinook: 42 m; chum: 16 m) and average daily maxima (Chinook: 130 m; chum: 58 m) were deeper than those of the other three species (Table 4). Among sockeye, pink (*O. gorbuscha*), and coho salmon, sockeye had the shallowest vertical distribution (average 3 m, average daily max 19 m), followed by pink (average 10 m, average daily max 37 m) and coho (average 11 m, average daily max 46 m). Maximum depths recorded from any tag were 83 m for sockeye, 74 m for pink, 97 m for coho, 253 m for chum, and 344 m for Chinook (the maximum depth

Table 4. Recorded depths, in meters, of 5 salmon species based on information from data storage tags recovered in the North Pacific Ocean from 1999 to 2006. N= sample size, Avg = average depth, Min = minimum depth, Max= maximum depth.

Species	N	Avg Depth	Avg Daily Min	Avg Night	Avg Day	Day-Night Difference	Avg Night Max	Avg Day Max	Avg Daily Max	Max
Sockeye	12	3	0	3	4	1	9	18	19	83
Pink	3	10	1	4	13	9	19	36	37	74
Coho	10	11	0	8	12	4	29	42	46	97
Chum	11	16	1	8	20	12	33	56	58	253
Chinook	2	42	17	40	43	3	84	125	130	344

the tag was capable of recording). A nonparametric Dunn multiple comparison test of the means of average depths for the three species with more than three tags (sockeye n = 12, chum n = 11, coho n = 10) showed the differences between each pair of species were highly significant (sockeye-chum Q = 53.51; sockeye-coho Q = 26.98; coho-chum Q = 24.64; Dunn $Q_{0.001,3}$ = 3.588; Zar 1984). Comparison tests of the average daily maxima for these three species were also highly significant.

Most fish displayed a diel pattern of vertical distribution, moving between shallower and deeper waters during the day and near the surface at night (average nighttime depths of 3–8 m), except for Chinook salmon. The diel pattern was strongest in chum and pink salmon, and was variably expressed, even in a single fish. The Chinook data are from two fish, one tagged as an immature and the other as a maturing fish. The tag from the immature fish had two years of data showing several different patterns of vertical distribution that changed seasonally; the fish remained below 100 m for one winter. Data from all other fish are from maturing fish in summer and fall.

DISCUSSION

During the marine phase of their life history, most Pacific salmon enter coastal waters, move offshore as they become larger, and move through coastal waters again as they return to their natal rivers. Some stocks, for example coho and Chinook stocks of western North America, may remain near coastal areas throughout their life. Vertical distributions can vary with these three main marine stages.

Juvenile Salmon

Studies of juvenile salmon in coastal areas indicated that young fish were generally very near the surface. Straty (1974) found that outmigrating Bristol Bay sockeye were at about 1 m at night and 2 m during the day. Over half of juvenile Oregon coho were caught within the top 2 m (Pearcy and Fisher 1988). In September, 80–90% of southeastern Alaska coho and Chinook juveniles were caught within 30 m of the surface (Orsi and Wertheimer 1995). More than 95% of juvenile coho in the Strait of Georgia were caught within

the top 45 m, 60–95% in < 15 m (Beamish et al. 2000). At a station sampled over a 24-h period 13 km southwest of the mouth of the Columbia River, most juvenile Chinook (89%) and coho (78%) salmon were in the top 12 m (Emmett et al. 2004).

Immature and Maturing Salmon in Offshore Waters

Orsi and Wertheimer (1995) found that larger Chinook juveniles could be caught at deeper depths, and deeper in fall than spring. This presages the greater depths at which immature and maturing salmon are found as they move to the wider offshore waters where they spend most of their lives and achieve the greater part of their growth. Manzer (1964) conducted some of the earliest investigations of salmon vertical distribution in offshore waters of the Gulf of Alaska in May–July. He found sockeye salmon mostly in the top 12 m at night and at 12 to 36 m during the day. Chum salmon were in the top 36 m at night and from the surface to over 60 m during the day. Both species were found to at least 60 m in May, but in June and July sockeye were limited to the top 36 m, possibly by the thermocline. There were no consistent differences by ocean age (-.2 and -.3) for either species. Few pink and coho salmon were caught, and both were "nearer the surface than sockeye and chum" (pink to 24–36 m; coho to 12–24 m).

In the western North Pacific, Machidori (1966) reported sockeye and chum salmon to be mostly in the top 20 m. French et al. (1971) caught sockeye, chum, pink, and coho salmon to 23 m (the deepest depth they fished) in spring and summer. Godfrey et al. (1975) reported most salmon were in the top 60 m, though a few coho and chum salmon were taken down to 80 m.

Tracking fish that carried ultrasonic tags allowed Ogura and Ishida (1992, 1995) and Ogura (1999) to gain insights into the detailed behavior of individual salmon in the central Bering Sea and North Pacific. Chum, pink, sockeye, coho, and Chinook salmon were all mostly within the top 50 m, and the first four species were primarily found shallower than 20 m. Chinook salmon were deeper (20–50 m) than other species. Coho salmon showed the clearest diurnal pattern of movement. Unfortunately, it was possible to track fish for only a few days (0.6 to 5.5 days).

Possible tagging or vessel effects may have obscured normal behavior.

The data we have presented on diel trawl surveys in the Bering Sea are consistent with these other findings. The great majority of fish caught were within the upper 40 m. Because the opening of the trawl is 40 m deep, finer resolution of vertical distribution was not possible.

There is very little winter data for vertical distribution of salmon in the open waters of the North Pacific and Bering Sea. Two hydroacoustic surveys in winter indicate that salmon of unidentified species in the open North Pacific were generally still within the top 40 m (Nero and Huster 1996; Sakai et al. 1997). Because salmon seem less abundant at night in these surveys, it may be concluded that they also continued their diurnal behavior pattern of vertical distribution and were near the surface (harder to detect with hydroacoustics) at night.

Data storage tags permit a longer-term look at what salmon do at sea. Nine tags on Japanese chum salmon also showed fish usually within the top 60 m, making deeper excursions during the day than at night (Wada and Ueno 1999; Azumaya and Ishida 2005; Tanaka et al. 2005). Depths over 80–100 m generally were not accessed until the fish neared Japan, when they occasionally descended to 150–360 m. These data are very similar to those we have retrieved from 11 data tags on chum salmon returning to Japan and Russia. The short intervals of data collection (every 5 s) on the tag analyzed by Tanaka et al. (2005) also allowed an accurate characterization of the daytime dives by chum salmon. They found fish made dives about 8.6 times per hour, with a duration of 5.1 min and 1.4-min intervals between dives. Fish were presumed to be feeding on prey which had moved deeper during daylight hours.

Immature and Maturing Salmon in Coastal Waters

Chinook salmon remaining in coastal waters throughout most of their lives may have different depth distributions. Data tags on Chinook in southeastern Alaska coastal waters showed several different diel patterns: no apparent pattern, nearer surface at night and deeper during the day, and deeper at night and nearer the surface during the day (Murphy and Heard 2001, 2002). Fish were generally within the top 60 m. Hinke et al. (2005) also found no consistent diel pattern, but discerned four different "habitats" or patterns of vertical distribution in data from 15 Chinook salmon off northern California and southern Oregon: a shallow night pattern around 10 m; a shallow day pattern at 0–80 m; a deep (mostly night) pattern around 55 m; and a deeper pattern around 100 m (60–280 m). Ocean age -.1 and -.2 Chinook salmon in southeastern Alaska were caught at deeper depths than juveniles (Orsi and Wertheimer 1995).

On the northeastern Bering Sea shelf, Russian trawl fisheries captured Chinook salmon incidentally at depths to 360 m throughout the year, and chum salmon in summer and fall

(Radchenko and Glebov 1997, 1998). The majority (90%) of Chinook were taken from 50 to 400 m, and were taken from slightly deeper areas from August to September. As in our analysis of eastern Bering Sea trawl data, they found older fish were more numerous in winter and younger fish were more abundant in the summer and fall. Erickson and Pikitch (1994) analyzed bycatch of Chinook salmon in US West coast trawl fisheries. Bycatches were larger in winter and were in a greater depth range (100–482 m), than in summer (< 220 m).

There have been a number of studies that shed light on behavior of maturing salmon as they return to coastal areas prior to spawning. A Japanese chum salmon moving along the eastern edge of the Kuril Islands to Hokkaido showed essentially the same behavior and vertical distribution (Ishida et al. 2001) as seen in the Bering Sea and North Pacific on our tags and those of other Japanese investigators (Wada and Ueno 1999; Azumaya and Ishida 2005). Data from a DST demonstrated a clear diel vertical movement pattern, with the fish within the upper 10 m at night and between the surface and 50 m during the day. When they enter the warmer (16°–20°C) coastal waters near Japan, chum salmon may move to very deep waters during the day. Japanese trawl fisheries in September–December encountered chum salmon at a range of 150–460 m, with most between 200 and 350 m (Ueno 1992, 1994). Fish were almost always captured during daylight hours, with few caught at night. This conforms to data from our data tags and those of Japanese scientists (Wada and Ueno 1999; Azumaya and Ishida 2005), where chum salmon entering coastal waters may spend several days with daytime excursions to several hundred m. These deepest dives were not found in DST studies of chum salmon in coastal waters of the island of Honshu, Japan, by Tanaka et al. (2000, 2001), possibly because the fish were likely past the deep dive phase of their migration, but fish frequently dove to 100–200 m. Deeper diving was most common in October and ceased by December as surface temperatures cooled and the thermocline shifted down. The inference is that fish were conserving energy by avoiding high surface temperatures (Tanaka et al. 2000).

In North America, a coastal trolling study in the Strait of Juan de Fuca demonstrated differences in depth of capture among species (Beacham 1986). Coho were closer to the surface than pinks and sockeye, which were in turn shallower than Chinook. A series of studies using ultrasonic tags tracked sockeye and Chinook salmon and steelhead trout (*O. mykiss*) in British Columbia coastal waters (Quinn 1988; Quinn et al. 1989; Ruggerone et al. 1990; Candy and Quinn 1999). Sockeye were in the upper 30 to 40 m, closer to the surface at night and slower swimming. The mean depth for Chinook was 70 m (usual range 7–200 m), with maximum depths between 300 and 400 m. The fish were generally at shallower depths during the day (25–64 m) than at night (49–78 m). Steelhead spent 72% of their time in the top 1 m, with few movements deeper than 7 m.

In fresh water, juvenile sockeye salmon in lakes are the only species that undertakes major vertical migrations. Patterns of migration vary across lake systems and with the age of fish, but in most populations, juveniles seem to move to the surface at dusk to feed, and are found deeper in the lake for much of the remainder of the day (overview in Quinn 2005). Reasons for vertical migration, including pursuit of prey, avoidance of predators, and thermoregulation, have been reviewed by Quinn (2005) and by Clark and Levy (1988) and Levy (1990), who postulated a framework including all three reasons. Growth (determined by feeding and temperature) was balanced against risk (predation). Immature and maturing salmon at sea are under similar constraints, but their pattern of vertical migration differs. In some lakes, juvenile sockeye descend again after dusk, while at sea, most salmon seem to remain near the surface. Brett (1971) hypothesized that lake surface temperatures may be too warm for the most efficient digestion and growth. Immature and maturing salmon at sea usually do not remain at depth during the day, but frequently return to the surface. It seems unlikely that their frequent and regular daytime vertical movements are due mainly to escape from predators, and descending speeds are slower than ascending speeds (Azumaya and Ishida 2005). Salmon may be descending in pursuit of food, because many of their prey (such as euphausiids, copepods, squid, and myctophids) undergo diurnal vertical migrations. Food is found in salmon stomachs throughout the day, although the occurrence of prey species may vary with time of day (Pearcy et al. 1984; Davis et al. 2000). Salmon may be feeding on prey whose daytime vertical range overlaps with their vertical foraging range. During the day, prey may be easier to see from below silhouetted against the lighter background above. Azumaya and Ishida (2005) concluded that regulation of body temperature was controlled by vertical movements and that maintenance of body temperature for growth and maturation may be a significant reason for the vertical excursions.

Results from data tags are generally in line with previously reported information. However, they illuminate some aspects of behavior, such as changes from relatively 'flat' behavior near the surface at night to movements up and down in the water column during daylight hours. This daytime movement shows that salmon do not move down to a fixed depth, but are in frequent vertical motion, meaning an "average" daytime depth, such as obtained from nets or hooks, may not give a full picture of the overall vertical distribution. Also, it does not seem that individual salmon are "stratified" during the day, with some near the surface and some deeper, but most are moving vertically. Data showing nighttime distribution close to the surface confirms that salmon are in very shallow waters, and confirms conjectures of why salmon abundance drops at night in surveys which use gear such as trawls and hydroacoustics which do not fully sample near surface waters (e.g., Nero and Huster 1996 and trawl data in this report). A survey that used surface gillnets (to 6 m) in day and night sets caught more fish at night (Manzer 1964), and commercial and research surface gillnetting by Japanese vessels is intentionally conducted with overnight deployment of surface gillnets because catches are higher (Ueno et al. 1969).

Data tags also allow a fuller picture of vertical distributions, with information on occasional or rare excursions to depths deeper than normal. Many other studies have been limited by depths fished, for example only setting nets to depths of 20 m or 40 m. While not common for sockeye, pink, and coho salmon, occasional movements to greater depths by these species show they are capable of using this part of the habitat. A more detailed analysis of salmon behavior is possible than with coarser sampling gear, such as deep gillnets or trawls with large vertical openings. While knowledge that distribution is within the top 40 or 60 m may be adequate for some purposes, knowledge of movements within that range may also be of use. The data from tags can either clarify or contradict some previous inferences. Manzer (1964) and Beacham (1986) found coho nearer the surface than sockeye and pink, while tag data indicate that sockeye have the shallowest distribution.

Better understanding of how salmon move through the ocean will require data throughout the marine residency. Detection of possible modifications in their vertical distribution due to factors such as competition and changes in ocean conditions will necessitate better baseline data now and continued monitoring in the future.

CONCLUSIONS

In coastal waters, we observed juvenile salmon near the surface, in depths that were usually < 15 m , and within the top 40 m when adults. In offshore waters, salmon are usually within the top 40 to 60 m, above the thermocline, but occasionally are found from 80 to 120 m deep. They usually were near the surface at night, and moved vertically during the day. Chum and Chinook salmon may go much deeper. Sockeye salmon seemed to have the shallowest vertical distribution, followed by pink, coho, chum, and Chinook salmon. There were many exceptions to these generalizations. Vertical movements may change daily, seasonally, or between years.

Limited hydroacoustic data on vertical distributions offshore in winter indicate that salmon were within the top 40 m, similar to depths in summer. Vertical ranges of Chinook salmon in coastal and shelf areas were deeper in summer in the Bering Sea, but deeper in winter off the U.S. West coast. Data from a Chinook in the Bering Sea displayed several different patterns of vertical distribution that changed seasonally.

Because of constant changes in vertical distribution, one must beware of limited term data such as catches of fish or short-term tracking. There is a need for more long-term data, throughout the marine residency of single fish, and for gear

that provides a fine enough resolution and complete coverage of salmon depths. Baseline data and monitoring will be needed to detect changes in vertical distributions over multi-year periods.

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Genetic Diversity and Population Structure of Chum Salmon in the North Pacific

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Abstract: Analysis of population structure and stock identification has been carried out by a number of different methods. In this study, we used SNPs in 730bp long sequences of the mtDNA COIII-ND3-ND4L region in order to examine genetic diversity and population structure of chum salmon in the North Pacific. In a total of 201 individuals analyzed, 48 from Korea, 44 from Japan, 45 from Alaska, 29 from Canada, 20 from Washington (USA) and 15 from east Sakhalin Island (Russia), as many as 55 variable sites comprising 51 different haplotypes were identified. Some of the haplotypes were population-specific so that they can be used for stock identification. Canadian and one of the Korean populations showed relatively high levels of haplotype diversity (h, 0.70±0.11 ~ 0.92±0.06) while Russian and one of the Korean populations showed low variability (h, 0.37±0.15 ~ 0.42±0.16). Pairwise FST and AMOVA analyses of the populations revealed that Korean and Japanese chum salmon are genetically indistinguishable and so are Russian, Alaskan, and Canadian salmon (FST < 0.1). Therefore, we suppose that the chum salmon populations in the North Pacific can be grouped, in general, into three genetic population units: a Korea-Japan unit, a Russia (east Sakhalin)-Alaska-Canada unit, and a Washington (USA) unit.

Keywords: chum salmon, genetic diversity, population structure, *Oncorhynchus keta*, ND3

INTRODUCTION

Stock identification and population structure analysis establish a basis for management of fisheries resources. Since molecular markers were introduced in stock assessment and conservation of salmon populations (Ferguson et al. 1995), microsatellite DNA (Beacham 1996; Beacham et al. 2003) and single nucleotide polymorphisms (SNPs; Sato et al. 2001, 2004) have recently been in use for such studies. SNP methods that use differences in DNA sequences are becoming more popular because of their easy standardization and application to high throughput assay systems (Brumfield et al. 2003; Melton 2003).

For chum salmon (*Oncorhynchus keta*) populations distributed widely in the North Pacific, Sato et al. (2004) examined SNPs in about 500bp sequences at the 5'end of the mitchondrial (mt) DNA control region. They analyzed as many as more than 2,100 individuals and found 20 variable sites defining 30 haplotypes. The variability appeared rather small (haplotype diversity, 0.63 ± 0.01) taking into account the relatively large number of individuals analyzed. Previ-

ously, Park et al. (1993) reported a low level of chum salmon intraspecific variation in the control region.

The present study investigated SNPs in the mtDNA COIII-(tRNA-gly)-ND3-(tRNA-Arg)-ND4L region, about 730bp long sequences. This region had been used for phylogenetic analysis of Pacific salmon (*Oncorhynchus*) (Domanico and Phillips 1995; McKay et al. 1995). Because it was known to have a high level of variability compared to other regions of the mtDNA (Thomas and Beckenbach 1989; Domanico and Phillips 1995), we also used this region in analyzing genetic diversity and population structure of chum salmon in the North Pacific.

MATERIALS AND METHODS

Samples

A total of 201 individual chum salmon were obtained from 11 populations on both sides of the North Pacific and in the Bering Sea (two Korean, two Japanese, one Russian (east Sakhalin), two Canadian, one Washingtonian (USA) and

three Alaskan populations) (Table 1; Fig. 1.). The sample size for each population ranged from 13 to 35 individuals. These numbers appear to be small, but in fact they are large enough for analysis of population diversity using nucleotide sequence data. Studies on optimal sequencing strategies for surveying molecular genetic diversity revealed that the realistic values for optimum sample size are relatively small, three to 10 (Pluzhnikov and Donnelly 1996), or 8 or fewer individuals (Felsenstein 2006). In addition, populations with the lower variability require a smaller sample size than more heterogeneous populations (Israel 1992).

The individual samples were collected when fish returned to their natal rivers. Liver or muscle tissues were taken from each individual and stored in ethanol until DNA extraction.

DNA Extraction and PCR Amplification

DNA was extracted from the stored specimens using a blood and cell culture DNA midi kit or a DNeasy tissue kit (Qiagen, Germany) following the manufacturer's protocol. The target DNA, COIII-ND3-ND4L region of the mitochondrial DNA, was amplified by PCR with the primer pair of COIII forward (5'-TTACAATCGCTGACGGCG-3') and ND4L reverse primers (5'-GGTGCGGTG AAACGC-GAGTC-3'). The reaction mixture consisted of Hotstar Taq polymerase (2.5unit, Qiagen), 10X PCR buffer (5 μl), 10mM each dNTPs (2.5 μl), 25 pmoles of each primer and 0.5–1.0 μg DNA. PCR procedures were as follows: preheating at 95°C for 15 min, followed by 35 cycles of denaturation at 95°C for 1 min, annealing at 50°C for 1 min, extension at 72°C for 1 min, and completion with final extension at 72°C for 10 min. PCR products were examined by 1% agarose-gel electrophoresis and purified by a PCR purification kit (Takara, Japan). The amplified DNA was either cloned into the vector pCR2.1-TOPO with the TOPO-TA cloning system (Invitrogen, USA) or directly sequenced. The insert DNA

or the purified DNA was sequenced using Automated DNA sequencer 377 or 3100 (Applied Biosystems, USA).

Population Genetic Data Analysis

The sequence data were aligned by ClustalW (Thompson et al. 1994). Haplotype diversity (h) and nucleotide diversity (π) were calculated using the ARLEQUIN program (Schneider et al. 2000). The extent of population subdivision was evaluated by analysis of molecular variance (AMOVA, Excoffier et al. 1992) and by estimation of pairwise F_{ST} values (Slatkin 1995). The Tamura and Nei model (1993) with a gamma distribution parameter alpha 0.3441 was applied in the AMOVA analysis.

RESULTS

Genetic Diversity

Nucleotide sequences of the mitochondrial DNA COIII-ND3-ND4L region were obtained in 201 individuals from two Korean (KS1 and KS2), two Japanese (JS1 and JS2), one Russian (east Sakhalin, RSC), three Alaskan (ALS1, ALS2 and ALS3), two Canadian (CS1 and CS2) and one Washingtonian (USA, AS) chum salmon populations (Table 1; Fig. 1). Comparison of the 730bp sequences revealed a total of 55 single nucleotide polymorphism (SNP) sites. These SNPs discriminate 51 different haplotypes (A1-A17, B1-B21, C1-C4, D1-D9; Table 2). Haplotype A1 is the most common sequence in Korean and Japanese populations but it is not observed in any other populations except a single individual in the Russian population. Haplotypes A2 through A17 that are differentiated from A1 by one or two nucleotides also occur only in Korean and Japanese populations. On the other hand, haplotype B1 is the most common sequence in Russian, Alaskan and Canadian populations. This haplotype is also observed in a few individuals in Washingtonian, Ko-

Table 1. Sampling locations with the latitudes and the longitudes, year of collection (Y) and the number of chum salmon samples (N).

| Sample name	Population	Y	Sampling location	Latitude / Longitude	N
KS	KS1	1999/2000/2001	Namdae River, KangwonDo	38.44'20"N, 128.37'17"E	6/14/15
	KS2	2000	Wangpi River, KyoungsangbukDo	36.59'23"N, 129.24'15"E	13
JS	JS1	1998/2000	Shokanbetsu River, Hokkaido	43.46'59"N, 141.31'59'E	2/22
	JS2	2000	Hakodate, Hokkaido	41.46'59"N, 140.45'00"E	20
AS	AS	1999/2000	Quilcene River, Washington	47.49'21"N, 122.52'28"W	6/14
CS	CS1	2000	Nitnat River, Vancouver Island	48.49'12"N, 125.06'00"W	14
	CS2	2001	Fraser River, British Columbia	49.06'00"N, 123.09'58'W	15
ALS	ALS1	1991	Noatak River, Alaska	66.58'53"N, 162.30'23"W	15
	ALS2	1994	Gisasa River, Alaska	65.15'44"N, 157.40'45"W	15
	ALS3	1995	American River, Alaska	65.25'30"N, 165.46'57"W	15
RSC	RSC	2003	Taranai River, Sakhalin	46'37'30"N, 142'26'00"E	15
Total					201
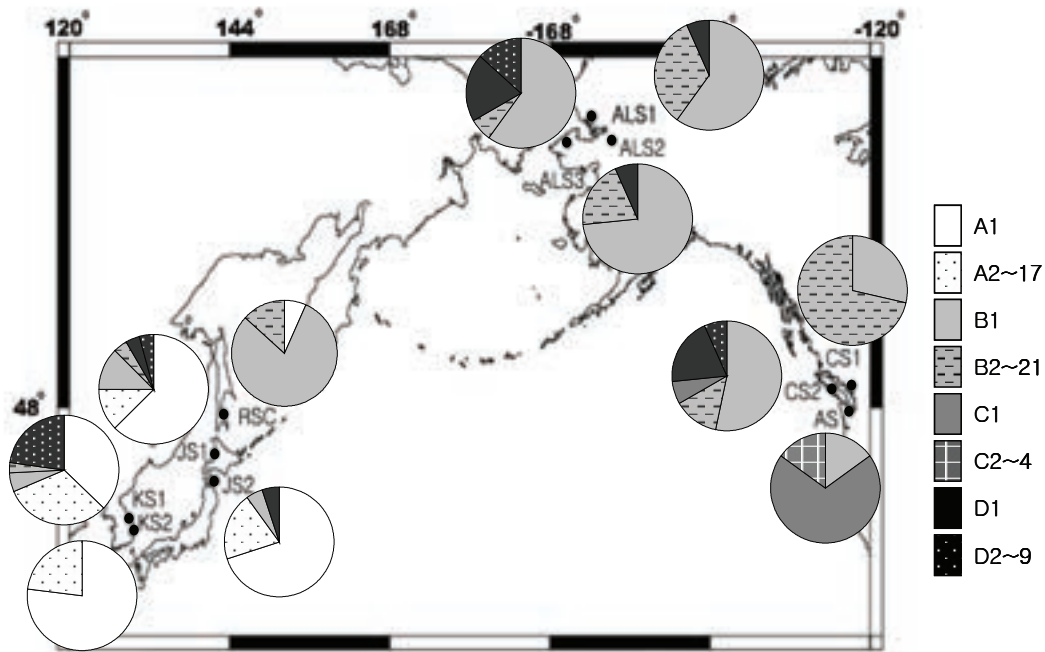
Fig. 1. Pie chart diagrams showing the haplotype frequency in each population of chum salmon.

rean and Japanese populations, showing its wide distribution around the North Pacific. B1 related haplotypes, B2 through B21, occur mostly in Canadian and Alaskan populations. Haplotype C1 and its derivatives, C2 to C4, occur almost exclusively in the Washingtonian population. Haplotype D1 is another common sequence observed in both eastern and western Pacific populations such as Japanese, Canadian and Alaskan populations. D1 derived haplotypes, D2 to D5, however, occur only in Korean populations. Haplotypes C1 and D1 are different from B1 by a single nucleotide.

Haplotype frequency distribution among the populations shows population-specific patterns of haplotype composition (Fig. 1). In Korean and Japanese populations, haplotype A1 and its related haplotypes, A2-A17, constitute more than 65% of the individuals, while in Russian (east Sakhalin), Alaskan and Canadian populations, haplotypes B1 and its related haplotypes, B2-B21, occur in more than 65% of the individuals. These haplotypes are found in Korean and Japanese populations at zero to 17%. On the other hand, the Washingtonian population consists of haplotype C1 and its differentiated haplotypes, C2-C4, in up to 85% of individuals (Fig. 1).

Haplotype diversity in each population ranges from 0.37 ± 0.15 to 0.92 ± 0.06 (Table 3). Relatively high levels of diversity were observed in Canadian (CS1, 0.92 ± 0.06; CS2, 0.70 ± 0.11) and one of the Korean populations (KS1, 0.84 ± 0.05). The other Korean population (KS2) and the Russian population (RSC) showed relatively low levels of diversity, 0.42 ± 0.16 and 0.37 ± 0.15, respectively. Japanese (JS1 and JS2), Alaskan (ALS1 to ALS3) and Washingtonian (AS) populations showed intermediate levels of diversity (0.47 to

0.64). The overall haplotype diversity among the populations turns out to be relatively high, 0.83 ± 0.02 (Table 3). Nucleotide diversities, however, are low in almost all chum salmon populations (0.00071 to 0.0053) as is the overall diversity (0.0036 ± 0.0013).

Population Differentiation

Pairwise F_{ST} values (Slatkin 1995) among the populations were significantly greater than zero ($p < 0.01$) in comparisons between any two of the populations except the comparisons between Korean and Japanese populations and between the Russian, Alaskan, and Canadian populations (Table 4). In these comparisons, the values were < 0.1, not significantly different from zero, even though the examined DNA was mitochondrial. These results suggest that Korean and Japanese populations are genetically indistinguishable as are the Russian, Alaskan, and Canadian populations. When the extent of population subdivision was evaluated by analysis of molecular variance (AMOVA, Excoffier et al. 1992), grouping the populations into three geographical groups, KS-JS/RSC-ALS-CS/AS, resulted in significantly strong levels of genetic structuring among the three groups (Table 5, $\Phi ct = 0.37$, $p < 0.05$). Other population groupings such as KS-JS/RSC-ALS/CS-AS and KS-JS/RSC-ALS-CS-AS did not show significant population structure among groups.

DISCUSSION

Single nucleotide polymorphisms observed in the mtDNA COIII-ND3-ND4L region in the present study were large

Table 2. Fifty-one different haplotypes and their distribution among 11 populations.

Haplotype	Locality											Total
	KS1	KS2	JS1	JS2	AS	CS1	CS2	ALS1	ALS2	ALS3	RCS	
A1	13	10	15	14	0	0	0	0	0	0	1	53
A2	1	0	0	0	0	0	0	0	0	0	0	1
A3	2	1	0	0	0	0	0	0	0	0	0	3
A4	1	0	0	0	0	0	0	0	0	0	0	1
A5	3	1	0	0	0	0	0	0	0	0	0	4
A6	1	0	0	0	0	0	0	0	0	0	0	1
A7	0	0	0	1	0	0	0	0	0	0	0	1
A8	1	0	0	0	0	0	0	0	0	0	0	1
A9	1	0	0	0	0	0	0	0	0	0	0	1
A10	0	0	0	1	0	0	0	0	0	0	0	1
A11	1	0	0	0	0	0	0	0	0	0	0	1
A12	0	0	0	1	0	0	0	0	0	0	0	1
A13	0	0	1	0	0	0	0	0	0	0	0	1
A14	0	0	0	1	0	0	0	0	0	0	0	1
A15	0	1	0	0	0	0	0	0	0	0	0	1
A16	0	0	1	0	0	0	0	0	0	0	0	1
A17	0	0	1	0	0	0	0	0	0	0	0	1
B1	2	0	3	1	3	4	8	9	11	9	12	62
B2	0	0	0	0	0	0	1	0	0	0	0	1
B3	0	0	0	0	0	0	0	2	0	0	0	2
B4	0	0	0	0	0	0	0	2	2	0	0	4
B5	0	0	0	0	0	0	0	1	0	0	0	1
B6	0	0	0	0	0	0	0	0	1	0	0	1
B7	0	0	0	0	0	2	0	0	0	0	0	2
B8	0	0	1	0	0	0	0	0	0	0	0	1
B9	0	0	0	0	0	0	0	0	0	1	0	1
B10	0	0	0	0	0	0	1	0	0	0	0	1
B11	0	0	0	0	0	0	0	0	0	0	1	1
B12	0	0	0	0	0	0	0	0	0	0	1	1
B13	0	0	0	0	0	1	0	0	0	0	0	1
B14	0	0	0	0	0	1	0	0	0	0	0	1
B15	1	0	0	0	0	0	0	0	0	0	0	1
B16	0	0	0	0	0	1	0	0	0	0	0	1
B17	0	0	0	0	0	1	0	0	0	0	0	1
B18	0	0	0	0	0	1	0	0	0	0	0	1
B19	0	0	0	0	0	1	0	0	0	0	0	1
B20	0	0	0	0	0	1	0	0	0	0	0	1
B21	0	0	0	0	0	1	0	0	0	0	0	1
C1	0	0	0	0	14	0	1	0	0	0	0	15
C2	0	0	0	0	1	0	0	0	0	0	0	1
C3	0	0	0	0	1	0	0	0	0	0	0	1
C4	0	0	0	0	1	0	0	0	0	0	0	1
D1	0	0	1	1	0	0	3	1	1	3	0	10
D2	5	0	0	0	0	0	0	0	0	0	0	5
D3	1	0	0	0	0	0	0	0	0	0	0	1
D4	1	0	0	0	0	0	0	0	0	0	0	1
D5	1	0	0	0	0	0	0	0	0	0	0	1
D6	0	0	1	0	0	0	0	0	0	0	0	1
D7	0	0	0	0	0	0	1	0	0	0	0	1
D8	0	0	0	0	0	0	0	0	0	1	0	1
D9	0	0	0	0	0	0	0	0	0	1	0	1
Total	35	13	24	20	20	14	15	15	15	15	15	201

Table 3. Haplotype diversity (h ± SD) and nucleotide diversity (π) in each population. N = number of samples.

Population	N	h (π)	Population	N	h (π)
KS1	35	0.8437 ± 0.0528 (0.003615)	CS2	15	0.7048 ± 0.1139 (0.001327)
KS2	13	0.4231 ± 0.1645 (0.000861)	ALS1	15	0.6381 ± 0.1288 (0.001054)
JS1	24	0.6087 ± 0.1118 (0.002216)	ALS2	15	0.4667 ± 0.1478 (0.000710)
JS2	20	0.5211 ± 0.1346 (0.001503)	ALS3	15	0.6286 ± 0.1253 (0.001402)
AS	20	0.5053 ± 0.1256 (0.000784)	RSC	15	0.3714 ± 0.1532 (0.000930)
CS1	14	0.9231 ± 0.0604 (0.005316)	Total	201	0.8286 ± 0.0188 (0.0036)

Table 4. Pairwise FST values among the chum salmon populations.

	KS	JS	AS	CS	ALS
JS	0.02850				
AS	0.34341*	0.45266*			
CS	0.19546*	0.28319*	0.25986*		
ALS	0.31521*	0.39329*	0.39681*	0.03347	
RSC	0.35041*	0.44361*	0.49551*	0.08399	0.01469

*$p < 0.01$

Table 5. Hierarchical analyses of molecular variance for chum salmon.

Source of variation	Variance component	Percentage of variation	F-statistics (Φ)
Among three groups (KS-JS/RSC-CS-ALS/AS)	0.1738	36.62	0.3662*
Among populations within groups	0.0093	1.97	0.0311*
Within populations	0.2915	61.42	0.3858*

*$p < 0.05$

enough to analyze genetic diversity and population structure of chum salmon. The level of sequence variability, 55 variable sites in about 730bp sequences (Table 2), turns out to be higher than those reported in the control region. Park et al. (1993) identified only four nucleotide variations in the entire D-loop region (approximately 1kb long) from an analysis of 29 individuals. Sato et al. (2004) found only 20 variable sites in about 500bp sequences at the 5'end of the control region from an analysis of more than 2,100 individuals. Haplotype diversity reflects a difference in variability. The overall haplotype diversities were 0.83(± 0.02) in the present study (Table 3) and 0.63(± 0.01) in Sato et al. (2004). Levels of haplotype diversities among populations show a different pattern between the two studies. In the present study, relatively high levels of haplotype diversities were observed in Canadian (CS1, 0.92 ± 0.06; CS2, 0.70 ± 0.11) and one of the Korean populations (KS1, 0.84 ± 0.05), while in Sato et al. (2004) Japanese populations showed higher levels of diversity (average, 0.63 ± 0.01) than any other populations. Diversities in Korean and North American populations were as low as 0.37 ± 0.08 and 0.34 ± 0.02, respectively (Sato et al. 2004). These contradictory results may result from different sampling strategies as well as the use of different molecular markers. Sato et al (2004) used a special strategy for sampling Japanese chum salmon in order to minimize human

influences on diversity such as transplantation and hatchery operations by avoiding sampling hatchery-released stocks. Such a strategy was not applied to other populations, e.g. for Korean chum salmon. Moreover, the two Canadian populations (CS1 and CS2) that showed high levels of diversity in the present study were not included in Sato et al (2004).

Differences in haplotype frequency distribution among populations and among some population-specific haplotypes are useful for identification of source populations in mixed-stock fisheries. For example, a high percentage of haplotype A1 in a catch shows the presence of either Korean or Japanese populations; the presence of haplotype D2 further distinguishes Korean populations from Japanese populations (Table 2; Fig. 1). A high percentage of haplotype C1 distinguishes Washingtonian populations from others. The present results were obtained from analysis of 11 chum salmon populations around the North Pacific. Further extensive studies on the COIII-ND3-ND4L sequences for more populations will increase the power of resolution for population discrimination in chum salmon.

Pairwise F_{ST} values (Slatkin 1995) among the populations suggest that Korean and Japanese chum salmon are genetically indistinguishable as are Canadian, Alaskan, and Russian salmon (F_{ST} < 0.1, Table 4). Results of analysis of molecular variance (AMOVA, Excoffier et al. 1992) further

support such a grouping of chum salmon populations: grouping the populations into three geographical groups, KS-JS/RSC-ALS-CS/AS, resulted in significantly strong level of genetic difference among the groups (Table 5, $\Phi ct = 0.37$, $p < 0.05$) as expected from the F_{ST} estimation. Therefore, the genetic structure of the chum salmon populations appears as follows: a Korea-Japan population unit, a Russia-Alaska-Canada population unit, and a Washington population unit. This population structure is reflected in the haplotype frequency distribution (Fig. 1). Korean and Japanese populations share haplotype A1 at no less than 37% of their individuals, and Canadian, Alaskan, and Russian populations share haplotype B1 at about 30%. The Washingtonian population has almost exclusively haplotype C1 and its derived haplotypes C2 to C4 (Table 2).

This population structure is partly supported by the results of Sato et al. (2004). Although they grouped populations based on geography and nation (i.e. Japan, Russia, and North America), the haplotype frequency distribution is somewhat consistent with the grouping of populations in the present study. In Sato et al. (2004), Korean and Japanese populations were characterized by a high frequency of the mtDNA control region with haplotypes A1, B3, and C1 (Table 3 in Sato et al. 2004). Russian and North American populations also have common features in that they share haplotype B3 with highest frequency but do not contain haplotype A1, which distinguishes them from the Korean-Japanese populations. One population in Russia, Primorye, which is located in the southernmost part of eastern Russia in the East/Japan Sea, is an exception -- this population contains haplotypes A1, B3, and C1 with a high frequency which is similar to the Korean and Japanese populations. Therefore, the Primorye population should be classified as a part of the Korea-Japan population unit. Washingtonian populations have features both common with and different from other North American populations in the mtDNA control region sequences (Sato et al. 2004). Although the Washingtonian populations possess haplotypes B3 and B13 common with the North American populations, they also have unique haplotypes B10, B14, and B16 (Table 3 in Sato et al. 2004).

The proposed population genetic structure in the present study is also consistent with the results of other genetic studies with minisatellite DNA (Taylor et al. 1994), restriction fragments and allozymes (Seeb and Crane 1999a,b). Minisatellite DNA variation among Japanese, Russian, northwest Alaskan (Yukon river), southeast Alaskan and British Columbian populations showed that Japanese populations are distinctively separated from the others ($D_2 > 30$, Fig. 5 in Taylor et al. 1994). Restriction enzyme site polymorphism in the ND5-ND6 region revealed that there are two major chum salmon groups in the North Pacific: Japanese populations and others including the Russian and Washingtonian populations (Table 6 in Seeb and Crane1999b). On the other hand, an allozyme study by Seeb and Crane (1999a) appears to show a different relationship in that an UPGMA tree showed a cluster of Russian and northwest Alaskan populations together with Japanese populations rather than with southeast Alaskan and British Columbian populations. However, the UPGMA tree topology was not statistically tested so that close affinities of Russian and northwest Alaskan populations to Asian populations cannot be corroborated. Multidimensional scaling analyses of the same data set in the same study and also in a successive study (Seeb and Crane 1999a,b), in fact, showed that there is clear distinction of Japanese populations from all the other populations. For the Washingtonian populations, separation from Alaskan and British Columbian populations was also shown in the allozyme studies (Seeb and Crane 1999a, 1999b). Although this separation was not as distinct as the one between Japanese and Russian-northwest Alaskan populations, the Washingtonian populations were a separate cluster in the multidimensional scaling plots and formed a separate clade by themselves in the UPGMA tree.

Differentiation of the three genetic population units may have occurred recently. The number of nucleotide differences between the haplotypes A1, B1 and C1, the representative haplotypes of each population unit, is limited to only one to three in about 730bp long sequences of the COIII-ND3-ND4L region. The overall nucleotide diversity among the populations is also as low as 0.0036 ± 0.0013, which is similar to the value observed in the mtDNA control region ($\pi = 0.0037$, Sato et al. 2004).

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Influence of Physical Parameters on Zooplankton Variability during Early Ocean Life of Juvenile Chum Salmon in the Coastal Waters of Eastern Hokkaido, Okhotsk Sea

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Abstract: Zooplankton variability during the early life of juvenile chum salmon and its relationship to physical environmental variability were studied from 2002 to 2004 in the Okhotsk Sea along the coast of eastern Hokkaido. During the study, the zooplankton taxa, Hydrozoa, Cladocera, Copepoda, Euphausiacea, Echinodermata and Appendiculata were commonly found. Cladocera, Copepoda, and Appendiculata were numerically dominant. At the boundary of the Soya Warm Current, the predominant zooplankton taxa shifted from Copepoda to Cladocera-Appendiculata. The predominant species of Copepoda, Cladocera and Appendiculata taxa were divided into two groups, based on their abundance and preferred water temperature and salinity. Group I was made up of cold-water species that prefer temperatures < 12ºC and salinities < 33.6 psu. Group II was made up of warm-water species that prefer temperatures >12ºC and salinities > 33.6 psu. Several species in Group I are important components in the diets of juvenile chum salmon. In Group I the cold-water copepod, *Pseudocalanus newmani*, was the most numerous species in Abashiri Bay from 2002 to 2004. Pelagic cold-water copepods (*Neocalanus* spp. other than *Neocalanus cristatus*) and neritic cold-water copepods (*Eurytemora herdmani* and *Tortanus discaudatus*) were more abundant in 2004 than in 2002 or 2003. We theorize that the abundance of pelagic copepods may be related to the timing of the retreat of sea ice, and that the abundance of neritic copepods may be related to the displacement of less saline water under the influence of terrestrial inputs. The Soya Warm Current, sea ice, and less saline water are thought to be key factors affecting zooplankton variability and, by extention, influencing the life modes of juvenile chum salmon in the Okhotsk Sea.

Keywords: Soya Warm Current, sea ice, low salinity, pelagic copepod, neritic copepod, spring blooms, zooplankton abundance

INTRODUCTION

Because the period of early ocean residence is thought to be a critical stage in the life history of anadromous salmonids, ocean conditions during this period may be important in determining their population size (Healey 1982; Bax 1983; Willette et al. 2001; Fukuwaka and Suzuki 2002). Zooplankton variability might be one of the most important factors affecting the survival of juvenile chum salmon (*Oncorhynchus keta*), because they habitually prey on zooplankton (Okada and Taniguchi 1971; Pearcy 1992; Mayama and Ishida 2003). According to the 'match / mismatch hypothesis' of Cushing (1990), fish survival depends on whether the

feeding stage of fish development synchronizes with the seasonal cycle of food production, or not. Seasonal changes in zooplankton abundance during the early life of chum salmon have been studied extensively (LeBrasseur 1969; Walters et al. 1978; Sibert 1979; Kaeriyama 1986; Asami and Hirano 1993; Seki 2005). The coasts bordering the Okhotsk Sea are covered with sea ice until early spring when the ice melts, and less saline water is mixed with meltwater and water from terrestrial sources (Ohtsuki 1982). By late spring, the Soya Warm Current (SWC) begins to prevail (Takizawa 1982; Aota 1984; Irie 1990). As a result, juvenile chum salmon in these coastal areas experience extreme changes in their ocean habitat. A previous study (Irie 1990) reported that juvenile

chum salmon that were affected by changes in coastal water parameters, rarely venture offshore into the Okhotsk surface water. Further, the study suggested that juvenile chum salmon disappear from coastal waters in July, when the SWC begins to prevail and zooplankton biomass simultaneously begins to decline. It is important to relate the succession of zooplankton communities by species to environmental changes along the Okhotsk Sea coasts, in order to better understand the early life history of chum salmon. Thus, we studied the relationships between zooplankton variability, physical conditions, and juvenile chum salmon populations in Abashiri Bay, near eastern Hokkaido, from 2002 to 2004.

MATERIALS AND METHODS

Study sites were located along four transects (A, B, C, D), each with stations 1 km, 4 km, and 7 km off Hokkaido's eastern coast in Abashiri Bay (Fig. 1). There were 12 stations in all with water depths ranging from 10–40 m. Surveys were conducted once every ten days from April to July, 2002–2004. Water temperature and salinity were measured with a Memory STD (Salinity-Temperature-Depth, Alec Electronics Co., Ltd.). Surface water temperatures were measured with a thermometer from surface bucket samples.

At the same time, water for analysis of chlorophyll-*a* concentration was collected from the surface at each station. One L of water was brought back to the laboratory in a cooled container. From this sample, 300 mL was filtered through a 47-mm Whatmann GF/F filter. The filters were frozen and stored for about one month before the chlorophyll-*a* was measured. Following the procedure established by Parsons et al. (1984), we measured chlorophyll-*a* concentrations with a Terner Desings fluorometer (Model AU-10).

Zooplankton samples were collected from near the bottom to the surface with a Norpac net (45-cm mouth and 0.33-mm mesh size). The net was towed vertically at about 0.5 m/s. Because a flow meter was not used with the plankton net, the volume filtered was calculated from tow depth. Water filtration efficiency was assumed to be 100%. After collection, zooplankton samples were immediately fixed in 5% buffered formalin. At the laboratory, a plankton splitter was used to divide samples into subsamples (Motoda 1959), depending on abundances, and a dissecting microscope was used to count the number of zooplankton (inds./m^3) in each taxon group and species.

RESULTS

The Physical Environment and Chlorophyll-*a* Concentrations

Average sea surface temperature (SST) at each coastal station fluctuated from 4.1 to 14.9°C in 2002, from 2.2 to 14.5°C in 2003 and from 5.7 to 16.4°C in 2004. SSTs were uniform at the 1-, 4-, and 7-km locations (Fig. 2a). SSTs in 2002 and 2004 showed similar fluctuations, except for the sudden decrease in late June 2002. In late April of 2003, we observed the lowest SSTs (2.6°C at one km, 2.4°C at four km, and 2.2ºC at 7 km offshore). Although the SSTs rose to 5–6°C by early May, lower SSTs continued until late May at
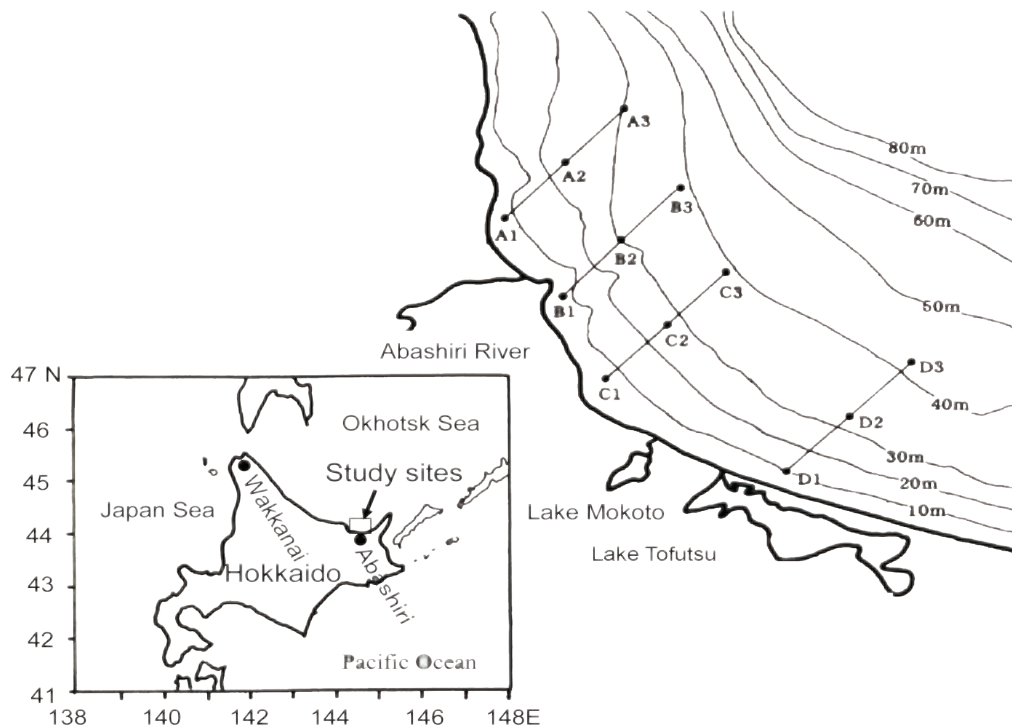

Fig. 1. Maps showing the study sites 1 km, 4 km and 7 km off the Abashiri coast in the Okhotsk Sea.

all locations in 2003.

Average sea surface salinity (SSS) varied from 32.0 to 33.6 psu in 2002, 31.1 to 33.7 psu in 2003, and 31.6 to 33.5 psu in 2004 (Fig. 2b). SSSs increased by early June at all locations in 2002. However, they decreased in mid-June. SSSs in 2003 fluctuated considerably compared to the other two years, especially at the one-km location. Although SSS in 2003 were very low from late April to late May, they began to increase in early June. In 2004, SSSs at 1 km and 4 km offshore showed similar fluctuations. Decreases in SSSs were observed in mid-May. In order to examine the SWC's impact on Abashiri Bay, we measured the average salinity at depths of 5 m, 15 m and 20 m offshore (Fig. 2c). The SWC appeared in early June and July of 2002, as indicated by a salinity value of 33.6 psu (Aota 1984) at 7 km offshore. Although the same salinity was not observed at 1 and 4 km offshore, these sites had highly saline water from mid-May to June (33.3–33.4 psu) at 1 km, and from early June (33.5 psu) at 4 km offshore. For the first time, the SWC was found from mid-June at 7 km offshore in 2003, and appeared from late June at four km offshore. Finally, it was detected in mid-July at 1 km offshore. The SWC appeared intermittently in 2004.

The first appearance of the SWC was observed in early May at seven km offshore. Thereafter in 2004, the SWC appeared from late June at all locations, except for 1 km offshore in mid-July.

Average surface chlorophyll (chl-*a*) concentrations from late April to mid-May fluctuated widely throughout the study (Fig. 2d). Although the highest chl-*a* (2.3 g/L) was found in late April 2002 at 1 km offshore, a clear peak was not detected in our investigations. In contrast with 2002, clear peaks were found in 2003 and 2004. Peaks in chl-*a* were observed in late April 2003 at both 4 and 7 km offshore. Chl-*a* peaked from late April to early May, reaching the highest levels at all locations in 2004.

Zooplankton Abundance and Taxonomic Composition

The average abundance of zooplankton at 1 km offshore were generally larger than at 4 or 7 km offshore (Fig. 3a). At 1 km offshore, zooplankton abundance peaked in late April $(5.1\times10^3$ inds./m^3) and mid-May $(6.3\times10^3$ inds./m^3) in 2002, in early May $(4.8\times10^3$ inds./m^3) and mid-June $(5.8\times10^3$ inds./m^3) in 2003, and in early May $(11.5 \times 10^3$ inds./m^3) and late
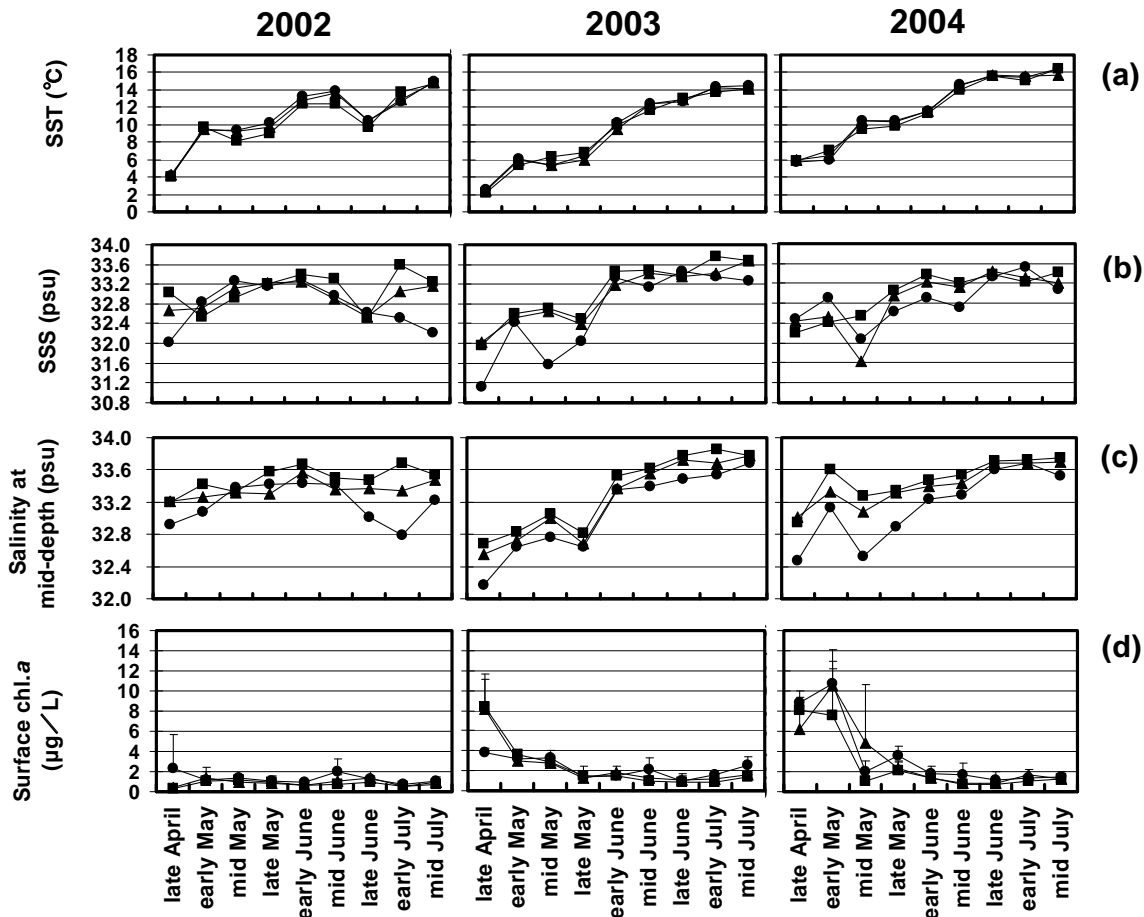

Fig. 2. Seasonal changes in averages of (a) sea surface temperature (SST), (b) sea surface salinity (SSS), (c) mid-depth salinity, (d) surface chlorophyll-*a* concentrations at 1 km (circles), 4 km (triangles), and 7 km (squares) off the Abashiri coast from 2002 to 2004. Bars in figure (d) indicate positive standard deviation.
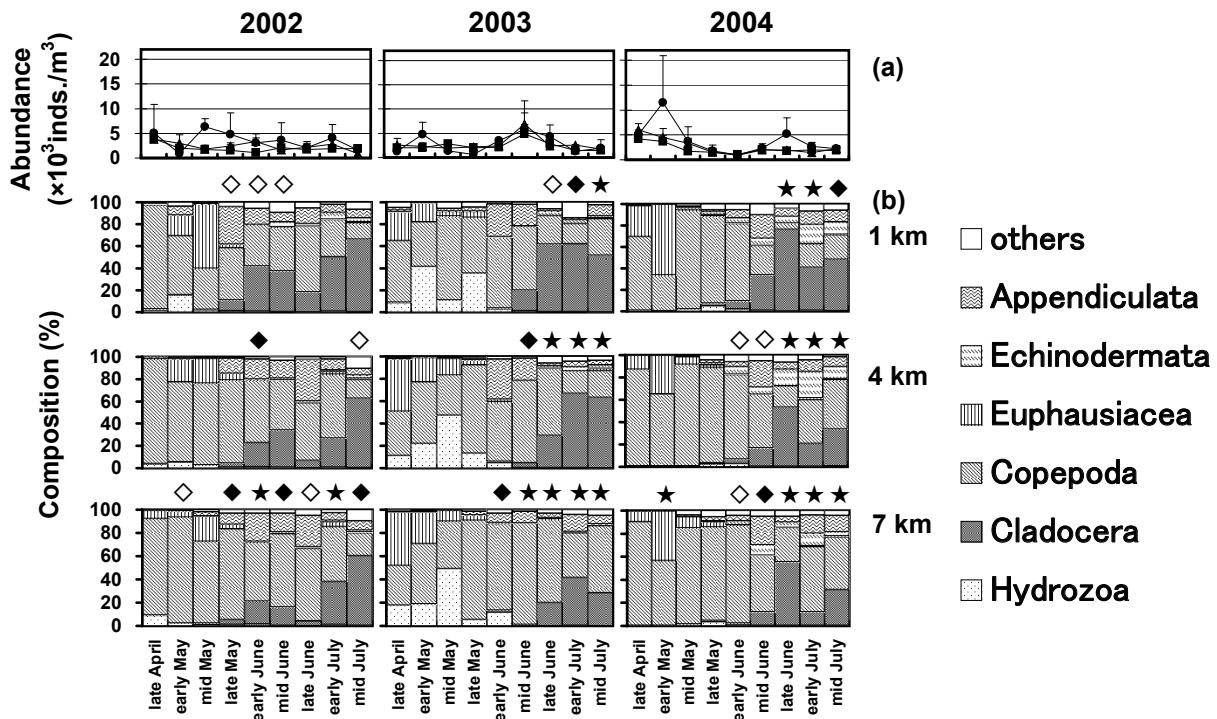
Fig. 3. Seasonal changes in averages of (a) total zooplankton abundance, (b) numerical composition of dominant zooplankton taxa at 1 km, 4 km and 7 km off the Abashiri coast from 2002 to 2004. In figure (a), bars indicate positive standard deviation. In figure (b), stars indicate observed SWC salinity ≧ 33.6 psu; filled diamonds indicate 33.5 psu; open diamonds indicate 33.4 psu at mid-depth at each location off the coast.

June (5.2×10^3 inds./m³) in 2004. The later-occurring maximums in 2002 and 2003 coincided with periods when water temperatures exceeded about 10ºC. With the exception of mid-June in 2003 and late June in 2004, total zooplankton abundances decreased gradually until mid-July of each year.

Six of the most numerous zooplankton taxa were the Hydrozoa, Cladocera, Copepoda, Euphausiacea, Echinodermata and Appendiculata (Fig. 3b). In these taxa, Cladocera, Copepoda and Appendiculata were always predominant. Hydrozoa predominated from late April to late May in 2003 at 1 and 4 km offshore. Hydrozoa made up 41% of the total zooplankton abundance in early May 2003 and thus contributed significantly to the earliest maximum in zooplankton abundance. Euphausiacea (mainly eggs) was the dominant taxon from early to mid-May in 2002, and from late April to mid-May in 2003 and 2004. Euphausiacea made up 58% of the total zooplankton abundance in mid-May 2002 at 1 km offshore, when the second maximum in zooplankton abundance occurred. In early May 2004, Euphausiacea made up 34–66% of the total zooplankton abundance at each location and contributed to the earliest maximum in zooplankton abundance. Echinodermata became sizeable enough to be counted after mid-June 2004 at all locations. Copepoda was one of the most important taxa throughout this investigation and were numerous until the appearance of the SWC (≥ 33.6 psu), especially in 2003 and 2004. Although the SWC appeared intermittently or not at all in 2002, Copepoda numbers usually decreased under high salinity conditions. How-

Table 1. List of dominant species including those comprising > 2% of total abundance of zooplankton. Open circles: warm-water species; solid circles: cold-water species; squares: eurythermic species; triangles: temperature preference not clear.

| Taxa		Species
Hydrozoa	□	*Rathkea octopunctata*
	△	*Obelia* sp.
Gastropoda	△	Unidentified larva
Cladocera	○	*Podon leuckarti*
	○	*Evadne nordmanni*
Copepoda	●	*Neocalanus* spp. other than *N. cristatus*
	○	*Mesocalanus tenuicornis*
	○	*Paracalanus parvus*
	●	*Pseudocalanus newmani*
	●	*Eurytemora herdmani*
	●	*Metridia pacifica*
	●	*Centropages abdominalis*
	●	*Acartia hudsonica*
	●	*Acartia longiremis*
	●	*Tortanus discaudatus*
	●	*Oithona atlantica*
Euphausiacea	●	*Thysanoessa inermis* egg
		T. inermis nauplius
		T. inermis calyptopis
		T. inermis furcilia
Decapoda	△	*Pinnixa* sp. Zoea
Echinodermata	△	*Echinopluteus* larva
	△	*Ophiopluteus* larva
Appendiculata	○	*Oikopleura longicauda*
	□	*Oikopleura dioica*
	●	*Fritillaria borealis* f. *typica*
Fish	○	*Enguraulis japonicus* egg
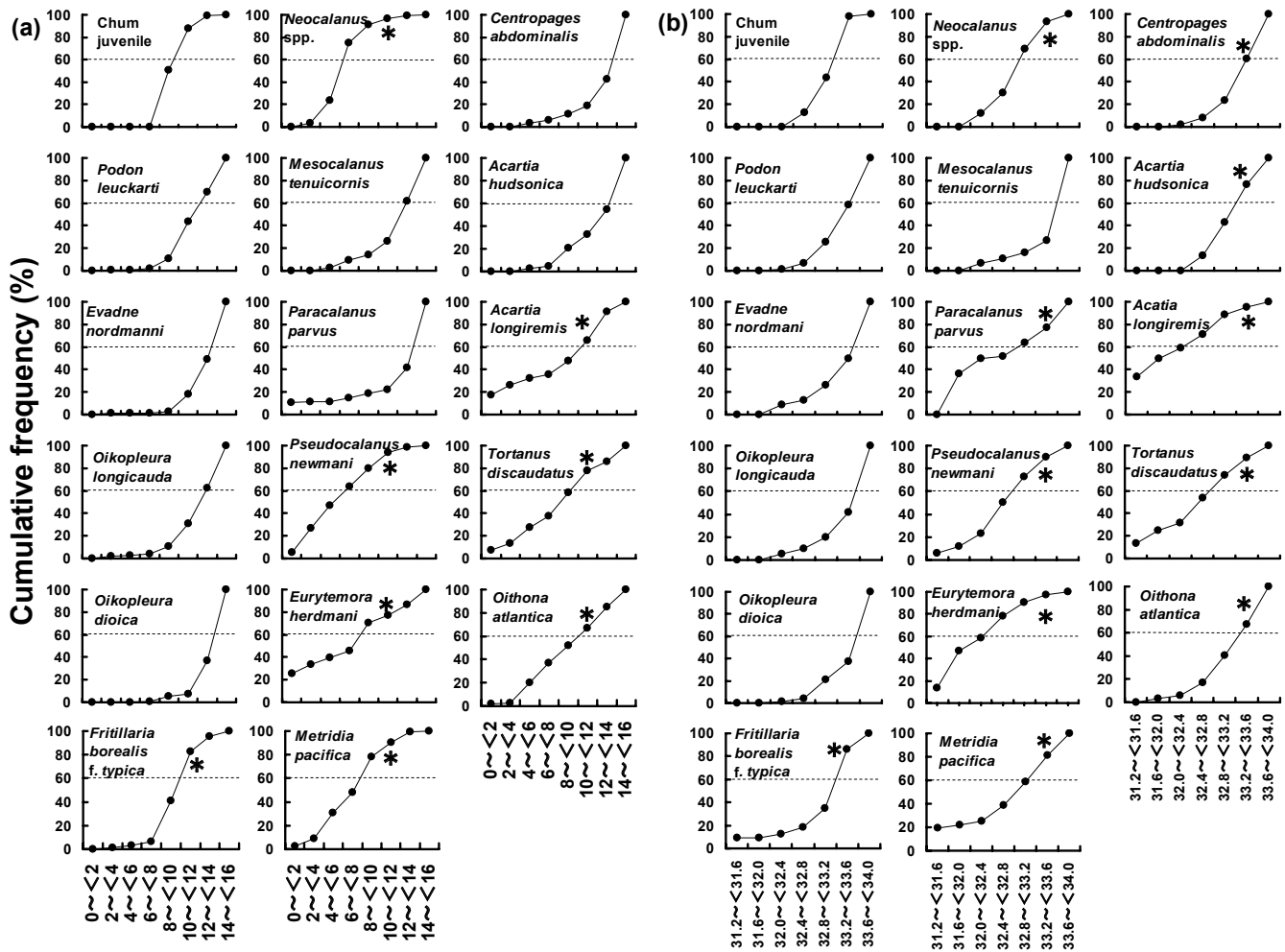
Fig. 4. Cumulative frequency distributions plotted against (a) water temperature and (b) salinity. All data from 2002 to 2004 are included. Water temperature and salinity throughout the water columns are averaged at 5-m intervals. Data for chum juveniles are taken from Nagata et al. (2007). Asterisks indicate species whose cumulative frequency reached 60% below 12ºC, and below 33.6 psu.

ever, as Copepoda declined, Cladocera and Appendiculata became more numerous, predominating from early June in 2002, early to mid-June in 2003, and mid- to late June in 2004. At 1 km offshore, Cladocera and Appendiculata made up 38% of the zooplankton in mid-June in 2003, and 84% of the zooplankton in late June in 2004. During our investigations, we observed that the composition of the zooplankton community in Abashiri Bay shifted from Hydrozoa, Euphausiacea and Copepoda to Cladocera and Appendiculata when the SWC appeared.

Table 1 indicates which species made up more than 2% of the total zooplankton at each coastal location from 2002 to 2004. Nine taxa and 24 species were defined as numerically dominant. Dominant species were mostly cold-water species. Cladocera, Copepoda and Appendiculata were common throughout the investigation (Fig. 3b).

Species Appearances Associated with Water Properties and Their Temporal Changes

In order to examine the relationships between the abundance of 16 species belonging to the three higher-order taxa Cladocera, Copepoda and Appendiculata, chum salmon juveniles, water temperature and salinity, the cumulative frequency distributions for each species were plotted against water temperature and salinity (Fig. 4). The cumulative frequency of chum salmon juveniles reached over 80% at a water temperature < 12°C and salinity < 33.6 psu. We chose the important species during the residence of chum salmon juveniles in the bay, whether the cumulative frequencies reached 60% or not at the boundary of a water temperature of 12°C and a salinity of 33.6 psu. As a result, for eight species (*Fritillaria borealis* f. *typica*, *Neocalanus* spp. other than *N. cristatus*, *Pseudocalanus newmani*, *Eurytemora herdmani*, *Metridia pacifica*, *Acartia longiremis*, *Tortanus discaudatus* and *Oithona atlantica*), the cumulative frequencies reached

60% below 12ºC. By contrast, for eleven species (*F. borealis* f. *typica*, *Neocalanus* spp. (other than *N. cristatus*), *Paracalanus parvus*, *Pseudocalanus newmani*, *E. herdmani*, *M. pacifica*, *Centropages abdominalis*, *A. hudsonica*, *A. longiremis*, *T. discaudatus* and *O. atlantica*), the cumulative frequencies reached 60% below 33.6 psu. From these results,

the dominant species were divided into two groups. Group includes species that showed a pattern similar to that of chum salmon juveniles and prefers water temperatures < 12°C and salinities < 33.6 psu. Group II includes species that prefer water temperatures > 12°C and salinities > 33.6 psu. Group I includes all cold-water species, and Group II includes al-
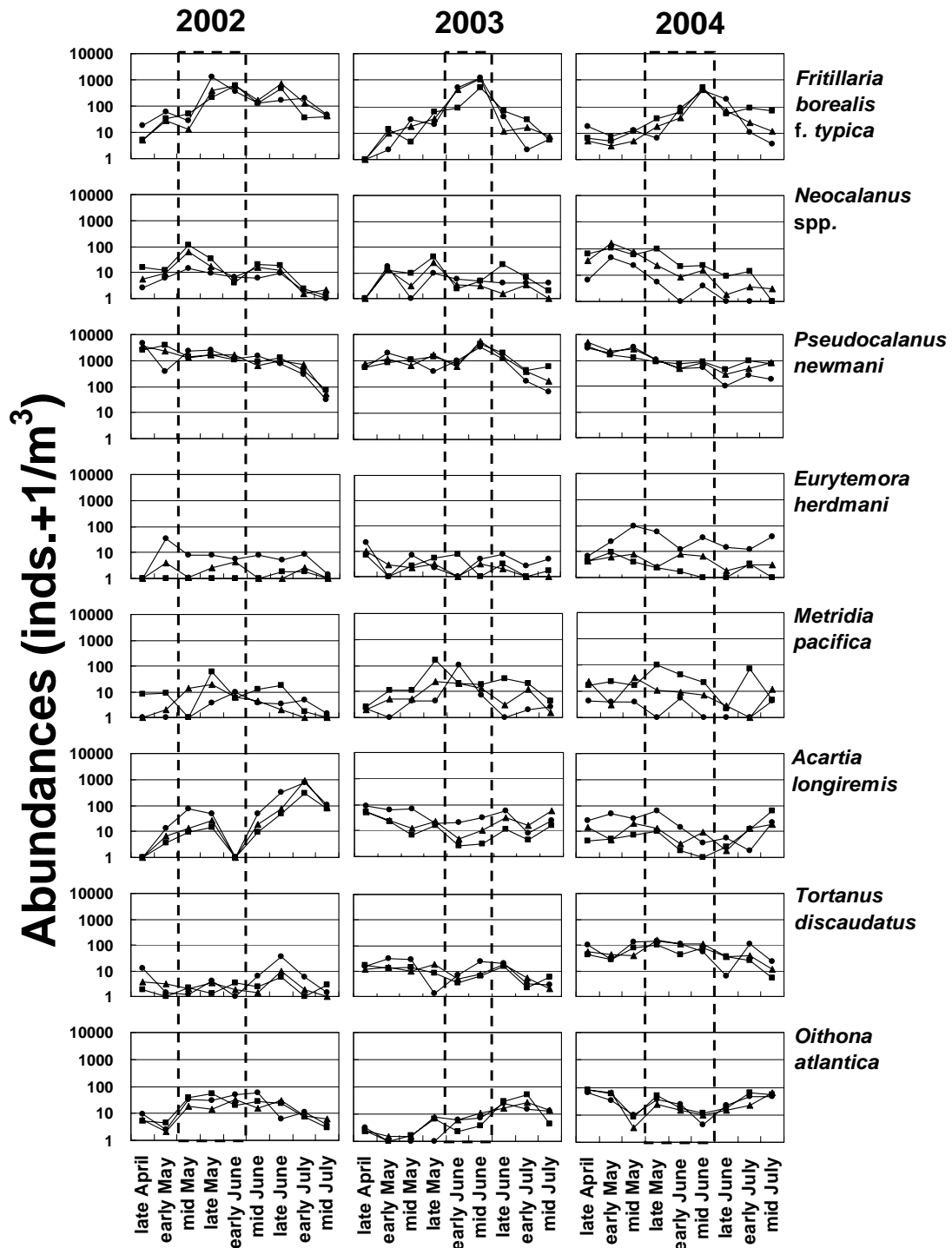

Fig. 5. Seasonal changes of abundances for species belonging to Group I from 2002 to 2004. Abundances are averaged at 1 km (circles), 4 km (triangles) and 7 km (squares) offshore. Dashed rectangles show the durations of chum salmon juvenile high CPUEs (Nagata et al. 2007).

most all warm-water species except for *C. abdominalis* and *A. hudsonica*.

Figures 5 and 6 indicate the seasonal average abundance of dominant species belonging to Groups I and II from 2002 to 2004, respectively. The fluctuations of *F. borealis* f. *typica* in 2002–2004 did not differ among locations (Fig.

5). This species increased from late April and peaked in late May to early June 2002, and in mid-June in 2003 and 2004. High abundance of *Neocalanus* spp. (other than *N. cristatus*) was observed in May and decreased rapidly thereafter in all years. *Neocalanus* spp. was more abundant at 4 and 7 km offshore. The maximum abundance was observed at 4
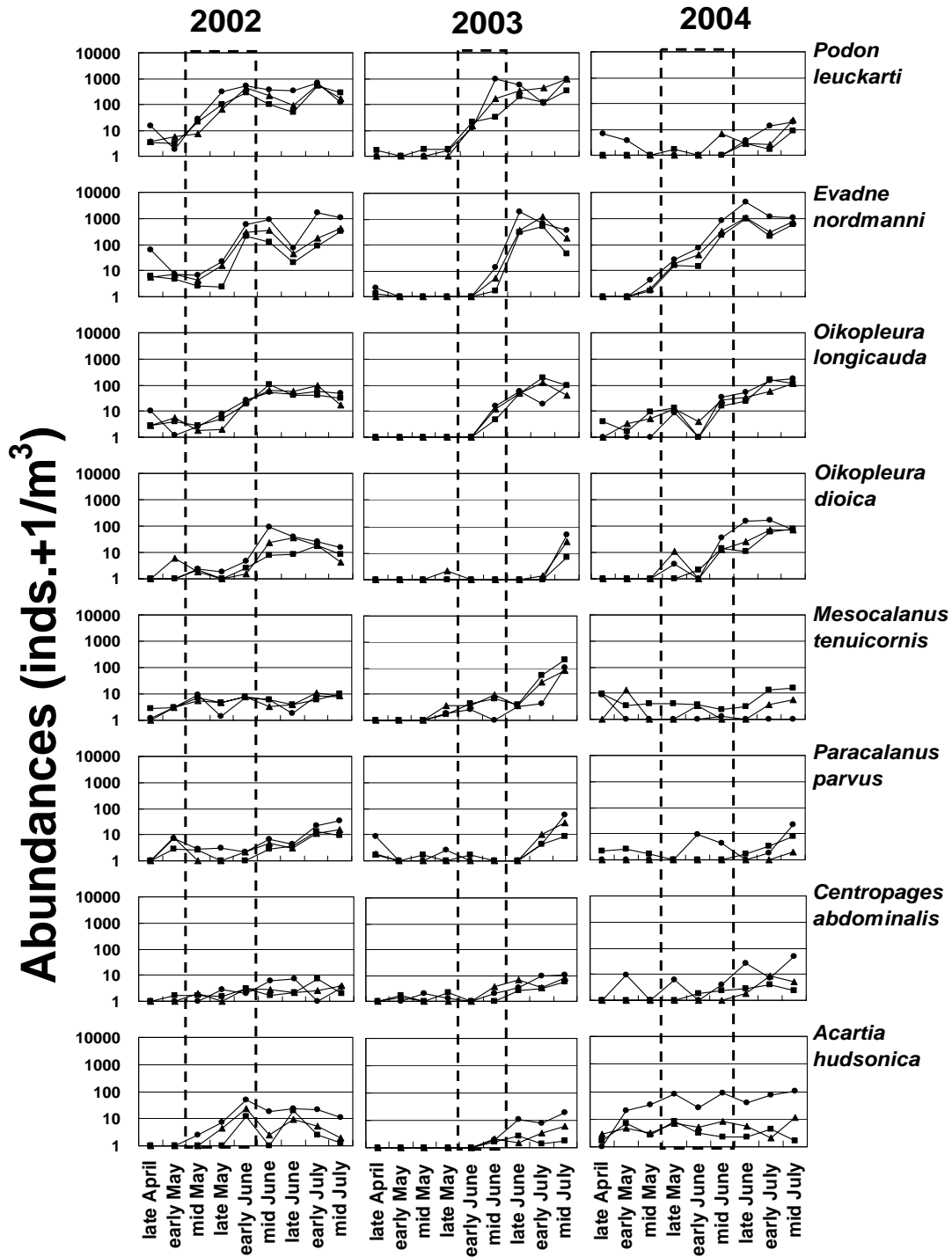

Fig. 6. Seasonal changes in abundance for species belonging to Group II from 2002 to 2004. Abundances are averaged at 1 km (circles), 4 km (triangles) and 7 km (squares) offshore. Dashed rectangles show the duration of chum salmon juvenile high CPUEs (Nagata et al. 2007).

km offshore in early May 2004. The abundance of *Pseudo-calanus newmani* did not differ among the three years at each location, and were the most numerous during our observations. High abundances ($>10^3$ inds./m^3) of *P. newmani* were observed from late April to late June in 2002 and 2003, from late April to late May in 2004. *Eurytemora herdmani* had < 10 inds./m^3 at each location in 2002 and 2003. However, a high abundance of this species was observed at 1 km offshore in 2004. *Metridia pacifica* was more abundant at 7 km offshore and peaked in late May in each of the three years. *Acartia longiremis* showed clear seasonal changes in 2002. This copepod increased from late April and peaked in mid-May, then increased from mid-June reaching a second peak in early July. *Tortanus discaudatus* was more abundant in 2004, especially at 1 km offshore and maintained an abundance of about 10^2 inds./m^3 from mid-May to early June. *Oithona atlantica* had abundances of $< 10^2$ ind./m^3 at each location in the three years and was distributed widely in the bay. Higher abundances were observed from mid-May to June 2002, early July 2003, and late April and July 2004. Through our investigations, chum salmon juveniles in 2004 could encounter high abundances of *Neocalanus* spp., *E. herdmani*, and *T. discaudatus*.

Abundances of the eight species belonging to Group II almost always increased in June or July (Fig. 6). Abundances of *Podon leuckarti* and *Evadne nordmanni* were higher at 1 km offshore and increased in June of all years, with the exception of *P. leuckarti* in 2004. Abundance of *P. leuckarti* in 2004 was very low (< 10 inds. /m^3). *Oikopleura longicauda* and *O. dioica* increased in June or July. Higher abundance of *Mesocalanus tenuicornis* were observed at 7 km offshore. In 2003, *M. tenuicornis* increased rapidly in July. *Paracalanus parvus* and *C. abdominalis* had < 10 inds./m^3, and increased in July at 1 km offshore. The abundance of *A. hudsonica* was $< 10^2$ inds./m^3 throughout 2002–2004. Higher abundances from late May to mid-July were found at 1 km offshore in 2004. Throughout our investigation, *Podon leuckarti* in 2002, and *E. nordmanni* and *A. hudsonica* in 2004 were more abundant than other species during the residence of juvenile chum salmon.

DISCUSSION

Coastal areas of Abashiri Bay in the Okhotsk Sea are seasonally affected by the SWC and sea ice (Takizawa 1982; Aota 1984). Further, terrestrial water flows into the bay resulting in a decrease in salinity (Ohtsuki 1982). The physical parameters studied in our surveys fluctuated significantly over time. The water temperature and salinity in the bay changed most drastically from late April to late May in 2003, decreasing from their usual levels. Such low water temperatures and salinity seem to be related to the timing of the retreat of sea ice. In 2003, sea ice remained in the bay for a longer time than usual (Japan Meteorological Agency), retreating on 28 April, the latest date among the three survey

years.

A few other physical events were observed in this study. For example, the salinity at each mid-level depth at each transect dropped suddenly from mid- to late June of 2002. Although the mechanism is not clear, such a decrease in salinity is thought to be caused by the influx of offshore surface water, because a decrease in SST was observed simultaneously with the drop in salinity. This phenomenon may have also weakened the influence of the SWC in 2002. A decline in salinity was also observed in mid-May in 2004. At that time, corresponding decreases in water temperature were not measured at any of the observation stations. This less saline water is thought to be caused by the input of terrestrial waters (Ohtsuki 1982). Finally, the SWC appeared suddenly in early May 2004 at 7 km offshore. It is known that the movement of the SWC is dependent on the differences in sea level between Wakkanai (the northernmost part of Hokkaido) and Abashiri (the eastern part of Hokkaido) (Aota 1984). The difference in sea level between Wakkanai and Abashiri increased suddenly in early May 2004 (Japan Oceanographic Data Center), so the movements of the SWC and accompanying phenomena are thought to be caused by the variation in sea level.

Spring phytoplankton blooms were not detected during the 2002 investigations. On the other hand, spring blooms were observed in late April 2003, farther offshore. Shimizu et al. (2000) reported that, in the northern Nemuro Strait of Hokkaido, spring phytoplankton blooms appeared soon after the sea ice had retreated from seasonally frozen coastal areas. Because we observed spring phytoplankton blooms as the sea ice retreated, Shimizu et al. (2000) may have been correct in his hypothesis. On the other hand, we observed spring blooms from late April to early May 2004, but the sea ice retreated on 24 March (Japan Meteorological Agency). Although the blooms' cause was not established in 2004, we observed less saline water (but not low temperatures such as in 2003) developed in the bay. Nutrient-rich water was also observed in late April (Sawada et al. 2006). The less saline water affected by terrestrial inputs might have prevailed in 2004, resulting in rich nutrients and spring blooms.

The SWC dynamics were thought to be an important factor, because we observed that the community succession patterns of zooplankton were closely related to the SWC's movements. Dominant species were divided into two groups at the boundaries of water temperature (12ºC) and salinity (33.6 psu (the level in the SWC)). Species belonging to Group I were composed of cold-water species and the timing of their appearance was similar to that of juvenile chum salmon. Several species were also identified in juvenile chum salmon diets (Nagata et al. 2007). Asami et al. (2005) suggested the high preferences for *Neocalanus* spp., *Metridia pacifica* and *T. discaudatus*. Pelagic calanoid copepods such as *Neocalanus* spp. are known to be an important food source for juvenile chum salmon as they move to open neritic waters (Simenstad and Salo 1980). Furthermore, *Neo-*

calanus spp. are large in size, and it is known that juvenile chum salmon begin to prey on larger zooplankton, when their fork length reaches 50–60 mm (Okada and Taniguchi 1971; Suzuki et al. 1994). Pelagic cold-water calanoid copepods, *Neocalanus* spp. were predominant in 2004. According to previous studies of *Neocalanus* spp. life cycles in the western, sub-Arctic Pacific Ocean (Kobari and Ikeda 2000), *Neocalanus* spp. complete ontogenetic migrations that coincide with phytoplankton production cycles in the surface layer, and grow more rapidly from the early to the late copepodite stages, synchronizing with spring phytoplankton blooms. Thus, occurrence of spring phytoplankton blooms in pelagic areas of the Okhotsk Sea may be key factor in the growth of *Neocalanus* spp. Shimizu (2005) postulated that the magnitude and timing of spring blooms were determined by the movement of sea ice in the Okhotsk Sea. When sea ice retreats earlier, spring blooms may appear earlier, and the zooplankton biomass may increase. According to the data of the Japan Meteorological Agency, the sea ice retreated earlier in 2002 and 2004 (24 March) than in 2003 (28 April). Although the sea ice retreated at nearly the same time in both 2002 and 2004, the ice remained for a shorter period of time in 2004 (54 days) than in 2002 (89 days). If Shimizu's hypothesis is applied to our study, we may theorize that high abundances of *Neocalanus* spp. in 2004 resulted from the early sea ice retreat. However, it is not clear how the sea ice influences zooplankton abundance when it remains in place. It is not also known how pelagic copepods move into coastal areas. However, there may be some hints. *Neocalanus* spp. increased in early May 2004, when the highly saline water (SWC) appeared. In contrast with *Neocalanus* spp., it is probable that *A. longiremis* was transported to the bay in offshore surface water, because *A. longiremis* became more numerous when water temperatures and salinity in the bay were low in June 2002. *Pseudocalanus newmani* was the most abundant species during our investigations. In southwestern Hokkaido, *P. newmani* appeared throughout the year in water shallower than 200 m and peaked in abundance after the spring blooms emerged: abundance decreased when water temperatures reached 15ºC (Yamaguchi and Shiga 1997). The spring distributions of *P. newmani* in Abashiri Bay might be similar to those seen in the Pacific Ocean, because *P. newmani* decreased when the SST reached 15ºC in mid-July. *P. newmani* was abundant in more distant areas in spring (Asami, unpublished data). It is suggested that *P. newmani* was distributed widely from coastal to offshore areas. In 2004, it was also discovered that common neritic species such as *E. herdmani* and *T. discaudatus* were particularly numerous from mid- to late May at one km offshore. *Eurytemora herdmani* is distributed in freshened sea water, and *T. discaudatus* can also withstand freshened water (Brodskii 1950). Higher abundance in 2004 may be related to the displacement of less saline water by terrestrial water inputs in late April and May. Resting eggs of zooplankton in bottom sediments were found along with *T. discaudatus* in coastal northern Califor-

nia (Marcus 1990). These eggs may play a potential role in the growth of local plankton populations. The changes in abundance of these species are controlled by local growth and reproduction, and high abundance occurs after a period of favorable growing conditions, which are determined largely by temperature and salinity. Within Group II *Podon leuckarti*, *Evadne nordmanni* and *O. longicauda* were also found in juvenile chum salmon diets (Nagata et al. 2007). Because the residence time of chum salmon juveniles overlapped the period of increased abundance of these species, juvenile chum salmon could utilize these species. *Acartia hudsonica* was more abundant in June and July 2004, although this species has not been described in diets of chum juveniles (Nagata et al. 2007). The occurrence of *A. hudsonica* in estuarine environments and the contribution of dormant eggs to plankton populations have been suggested in Maizuru Bay of Honshu, Japan (Ueda 1987). It may be that displacement of less saline water in 2004 might be related to the appearance of this species along with *Eurytemora herdmani* and *T. discaudatus*, creating favorable conditions for growth.

Throughout our investigations, the features of several copepods' appearance in 2004 were different from 2002 and 2003. Only horizontal abundances of zooplankton are described in the present study. Because chum salmon juveniles are distributed in the surface layer (Moulton 1997), the zooplankton vertical distributions must be also studied in order to explain why and how the species are utilized (e.g. Seki 2005).

The movement and composition of the SWC, sea ice and less saline water affected by terrestrial inputs may have been factors influencing zooplankton variability during the early life of juvenile chum salmon in the Okhotsk Sea. The growth of juvenile chum salmon population was greatest in 2004 (Nagata et al. 2007). In the future, biological analyses of returning adult salmon may prove a link between zooplankton variability and growth or mortality of chum salmon in their early life.

ACKNOWLEDGEMENT

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Influence of Coastal Seawater Temperature on the Distribution and Growth of Juvenile Chum Salmon, with Recommendations for Altered Release Strategies

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Abstract: In 2002 we initiated a project to determine the optimal timing for releasing juvenile hatchery chum salmon in rivers along the northeast coast of Hokkaido in northern Japan. Otolith-marked juveniles released in mid May 2002 and 2004 were captured by a surface trawl net 1 km off the coast in late May. In contrast, juveniles released in mid May 2003 were not observed in coastal waters until early June, along with chum released in late April of the same year; fish from these releases were captured in littoral areas in mid/late May with beach seines. In addition, early growth rates for juveniles released in late April 2003 and subsequently captured 1 km off the coast were lower than for juveniles released in mid-May. Juvenile chum rapidly disappeared from coastal waters after late June when sea surface temperatures (SST) were > 13°C. While relatively high juvenile abundances were found in coastal waters from May to June in 2002 and 2004, when SST ranged from 8 to 13°C, this water temperature range occurred in coastal waters only in June 2003. In contrast, SSTs from 7 to 12°C were found in the littoral zone in May 2003. Offshore marine movement of juvenile chum appears to depend on seawater temperature rather than fish size, especially considering that water temperatures < 8°C appeared to restrict movement offshore. We caution against releasing juvenile chum salmon when coastal water temperatures are < 7°C or > 11°C.

Keywords: ALC marking, hatchery chum salmon, SST, spatial distribution, abundance, growth, zooplankton, stocking strategy

INTRODUCTION

The number of adult hatchery-origin chum salmon (*Oncorhynchus keta*) in Hokkaido increased from ~10 million in the middle 1970s to ~40 million in the 1980s as a result of successful hatchery programs and favorable ocean conditions (Kaeriyama 1999). During the 1990s, the chum population fluctuated between 27 and 65 million with marine survivals varying between 2.6 and 5.9% (Nagata and Kaeriyama 2004). Marine survival differs among areas. Recent survival for salmon returning to the Okhotsk Sea has been much higher than those for fish returning to the Japan Sea and the Pacific Ocean regions of Hokkaido. As well, early migrating chum survived at higher rates than late-run groups (Nagata et al. 2004).

Salmon recruitment is determined largely by early mortality (Bax 1983; Willette et al. 2001; Fukuwaka and Suzuki 2002; Mueter et al. 2002). The match or mismatch between the release of larvae and the production of their food influ-ences recruitment success (Cushing 1990). Pink salmon (*O. gorbuscha*) survivals in Prince William Sound were high in years of extended copepod blooms (Willette et al. 2001). In Hokkaido, chum salmon populations have been maintained by hatcheries with similar numbers of juveniles released (approximately one billion) every year during the past twenty years. Because chum returns varied during this period, we hypothesize that these fluctuations were caused by coastal water conditions that affect food production and predation. If our hypothesis is true, it may be appropriate to alter stocking strategies to reduce variations in the numbers of returning chum salmon. Hokkaido hatchery managers typically release chum juveniles when coastal seawater temperatures are between 5 and 13°C (Seki 2005). In order to evaluate the influence of temperature at the time of release, we investigated the spatial distribution, growth and diet of hatchery-produced chum salmon in relation to coastal water conditions, especially temperature.

MATERIALS AND METHODS

Otolith Marking and Fry Release

Approximately 34 million hatchery chum juveniles are released annually into the Abashiri River, usually during May (Fig. 1). To investigate how abundance, distribution, and growth are influenced by the coastal environments, eyed-eggs were marked by immersion in 200 ppm alizarin complexone (ALC) solution for 24 h as described by Tsukamoto (1988) and Nagata et al. (1995). Small single (S), large single (L) and double (D) band ALC otolith marks were produced (Table 1).
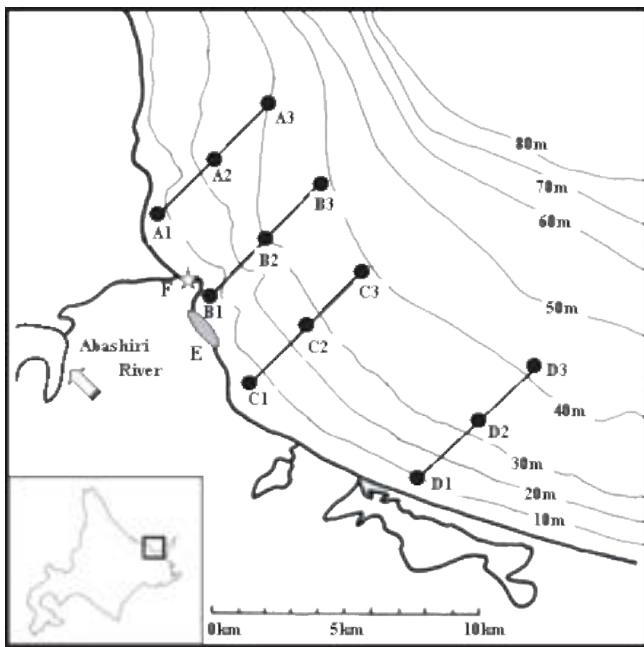
Fig.1. Maps showing the study sites at the fishing port (F), the littoral area (E), and 1 km, 4 km and 7 km off the Abashiri coast (A–D) in the Okhotsk Sea. Arrow shows the release site for ALC-marked chum juveniles.

To evaluate inter-annual differences, we used eyed eggs fertilized in mid to late October that were marked with S (2003, 2004) or L (2002) bands and fed artificial feed in raceway ponds. Mean fork lengths (MFL) and body weights (MBW) from 2002 to 2004 were 46.6 mm and 0.87 g, 47.5 mm and 0.96 g, and 48.0 mm and 1.08 g, respectively. In mid May of 2002, 2003, and 2004, 2 million, 1.4 million, and 0.8 million, respectively, marked juveniles were released at Lake Abashiri near the outlet of the Abashiri River (Fig. 1).

Additional releases were made in 2003 and 2004 to investigate the influence of the timing of release on distribution patterns and growth. One million marked juveniles (47.5 mm MFL and 0.99 g MBW) with an L band in the otolith were released in late April 2003 to compare with fish released in mid May the same year. In 2004, eggs that had been incubated in low and high temperature water to produce two groups of similar sized individuals were released in mid May (0.9 million L-marked juveniles, 46.8 mm MFL and 0.90 g MBW) and late May (0.7 million D-marked juveniles, 47.9 mm MFL and 0.97 g MBW), respectively.

Sampling Survey and Biological Analysis

Twelve study sites were established along 3 transects on the Abashiri coast (Fig. 1). Four sites (A1, B1, C1 and D1) were along a transect 1 km offshore, 4 sites (A2, B2, C2 and D2) were 4 km offshore and the final 4 sites (A3, B3, C3 and D3) were 7 km offshore. Water depths at the transects 1, 4, and 7 km offshore were 10–15 m, 20–30 m, and 30–40 m, respectively. Juvenile chum were collected with a surface trawl net (8-m-wide x 5-m-deep mouth, 18 m long with wing nets 7 m long and a central bag with 5-mm mesh) towed through the 1–2 m surface layer for 1–2 km at 4–6 km/h during the day (5:00–14:00) at intervals of 10 days from late April to early July (2004) or to mid July (2002 and 2003). Rough weather prevented sampling on a few occasions. One additional site at the Abashiri fishing port was sampled in

Table 1. Date, number and fish size of alizarin complexone (ALC)-marked chum salmon juveniles stocked in the Abashiri River from 2002 to 2004. Recapture rate of each marked group in the coastal and littoral waters from 2002 to 2004. Recapture rate was computed as the number of recaptured juveniles to one million marked juveniles.

Marked group[1]	Date of fertilization	Date of release	Stocked number of marked fish	Mean fork length (mm)	Mean body weight (g)	Number of recaptured fish		Recapture rate (number / million juveniles)	
						Coast[2]	Littoral	Coast	Littoral
ALC (L)	26 Oct. 2001	17 May 2002	2,009,000	46.62	0.87	1,923	-	957	-
ALC (L)	23 Sep. 2002	28 Apr. 2003	1,870,000	47.46	0.99	779	363	417	194
ALC (S)	24 Oct. 2002	15 May 2003	1,385,000	47.48	0.96	794	97	573	70
ALC (S)	15 Oct. 2003	16 May 2004	784,000	47.95	1.08	611	13	779	17
ALC (L)	15 Nov. 2003	16 May 2004	886,000	46.79	0.90	379	3	428	3
ALC (D)	15 Nov. 2003	30 May 2004	671,000	47.90	0.97	88	0	131	0

[1] L, S and D represent single large ALC-banding, single small ALC-banding and double ALC-banding marks, respectively.
[2] The number shows the sum of fish recaptured from 1 km to 7 km.

late May 2003 with a trawl net that was towed for 0.5 km.

Use of the nearshore littoral zone was evaluated using a beach seine (3.5-m-wide x 2-m-deep mouth, 10 m long with wing nets 3 m long and a central bag with 3-mm mesh) from 2002 (only in late May) to 2004. Five seine sets were usually made, starting 100 m offshore, at intervals of 50–100 m along the beach.

Captured fish were sacrificed by an overdose of MS 222 to prevent regurgitation or defecation, preserved in 5% neutralized freshwater formalin, and transferred to 70% ethanol after 12–24 h. Some fish were released soon after they were measured. Catch per unit effort (CPUE) for the surface trawl net was expressed as the number of chum juveniles caught per 2-km tow.

Chum juveniles at each study site were measured for fork length and wet body weight, to the nearest 1 mm and 0.01 g, respectively. Otoliths were examined for ALC-marks using ultraviolet (UV)-light microscopy without polishing the otolith surface except when it was difficult to identify different marks because the surface of otolith was unclear. Full and empty stomachs were weighed to the nearest 0.0001 g to calculate the weight of stomach contents. The percent stomach content index (SCI) was calculated as: (weight of stomach contents) / (body weight) x 100. Diet composition was determined using a binocular microscope.

Statistical Analysis

Arcsin square-root transformed fork length and SCI data were compared by one-way analyses of variance (ANOVA). Specific growth rates were calculated as the slope (b) of the growth curve ($L_t = a \, e^{bt}$, where L_t is the fork length at time t). We used fork lengths of marked juveniles at release and recapture and compared among groups and years using analysis of covariance (ANCOVA). When significant differences were found, multiple comparisons were made using Scheffe's test (Zar 1984).

Electivity indices (E) for food preference were calculated as E = (ri - pi) / (ri + pi - 2ripi), where ri is the proportion of i prey animal consumed by fish and pi is the proportion of the i animal available at a study site (Jacobs 1974). Electivity ranged from -1 to +1; -1 indicates the strongest negative preference, +1 the strongest positive preference. Zooplankton data collected at the coastal study sites and reported by Asami et al. (2007) were used for analysis.
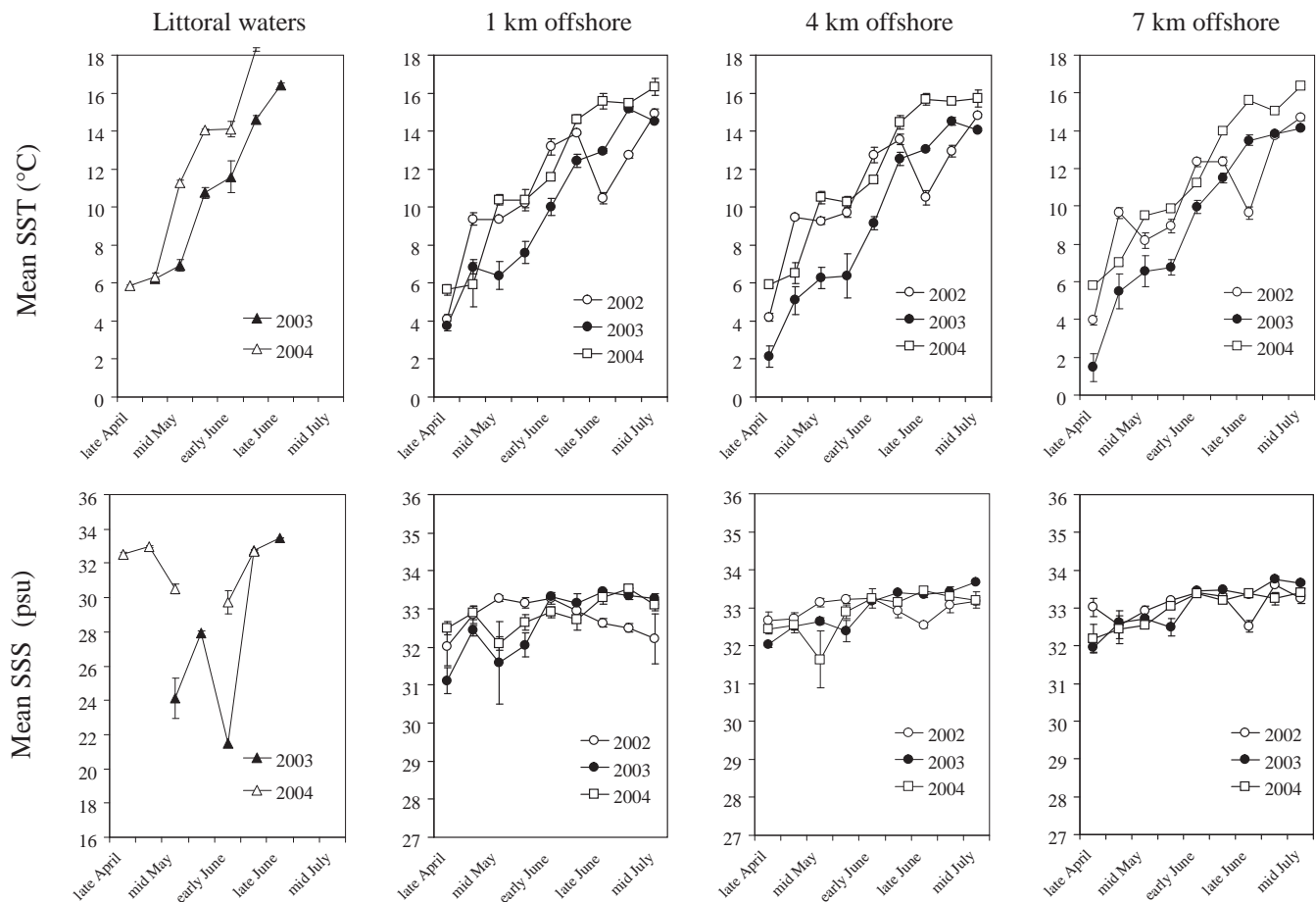

Fig. 2. Changes in mean values of SST and salinity at the littoral sites, and the 1-km, 4-km and 7-km offshore transects in the Okhotsk Sea from 2002 to 2004. Bars indicate standard errors.
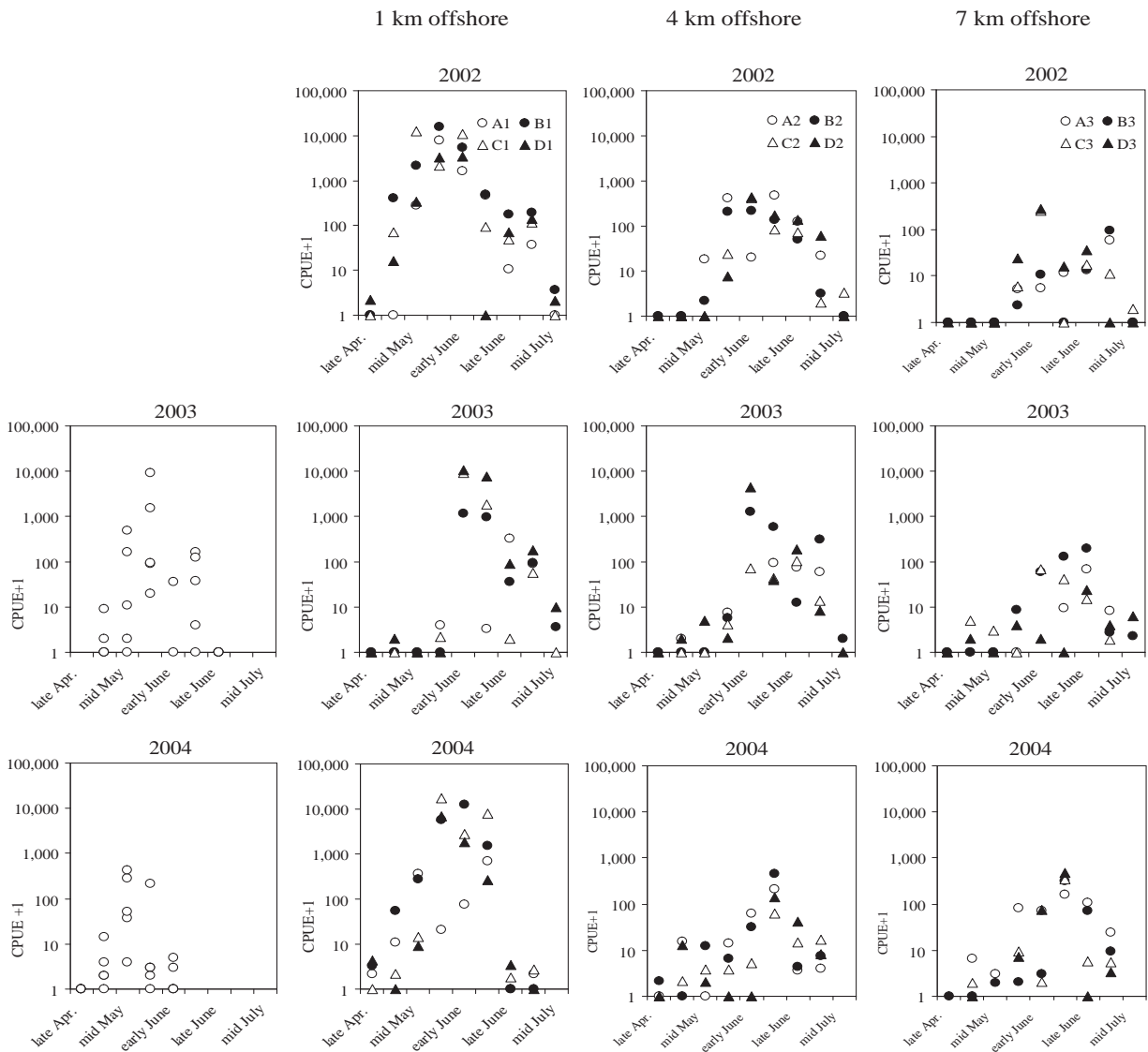
Fig. 3. Changes in CPUE (catch per unit effort, the number of juveniles per 2 km towing or per beach seine) of unmarked juvenile chum salmon captured at the littoral sites (beach seine), and at the 1-km, 4-km and 7-km offshore transects (trawl net) in the Okhotsk Sea from 2002 to 2004.

RESULTS

SST and SSS

Sea surface temperatures (SSTs) increased seasonally at all sites, except in 2002, which experienced cooling in late June that persisted until early July. Two thousand three was generally cooler than 2002 and 2004 until late June. Water in the littoral area warmed up more rapidly than offshore waters (Fig. 2).

Differences in sea surface salinity (SSS) among sites and locations were less pronounced than temperature differences (Fig. 2). SSSs generally increased as the seasons progressed.

Distribution and Numbers of Juveniles

Although sampling effort was relatively constant among years, far fewer fish were captured in coastal waters from May to July 2003 (~40,300) than in the other two years (~72,000 in 2002 and ~61,600 in 2004). In contrast, the number of juveniles in littoral waters in 2003 was ~11,900, exceeding the ~1,000 caught in 2004.

CPUEs for unmarked chum were generally highest in June, and decreased with distance from shore (Fig. 3). CPUEs at the 4- and 7-km offshore transects peaked later than those 1 km offshore. Almost no unmarked juveniles were captured in May 2003 when SST was < 8°C. However, in May many juveniles were found in littoral areas and at the fishing port (only one survey in late May). Chum abundance in May 2004 in the
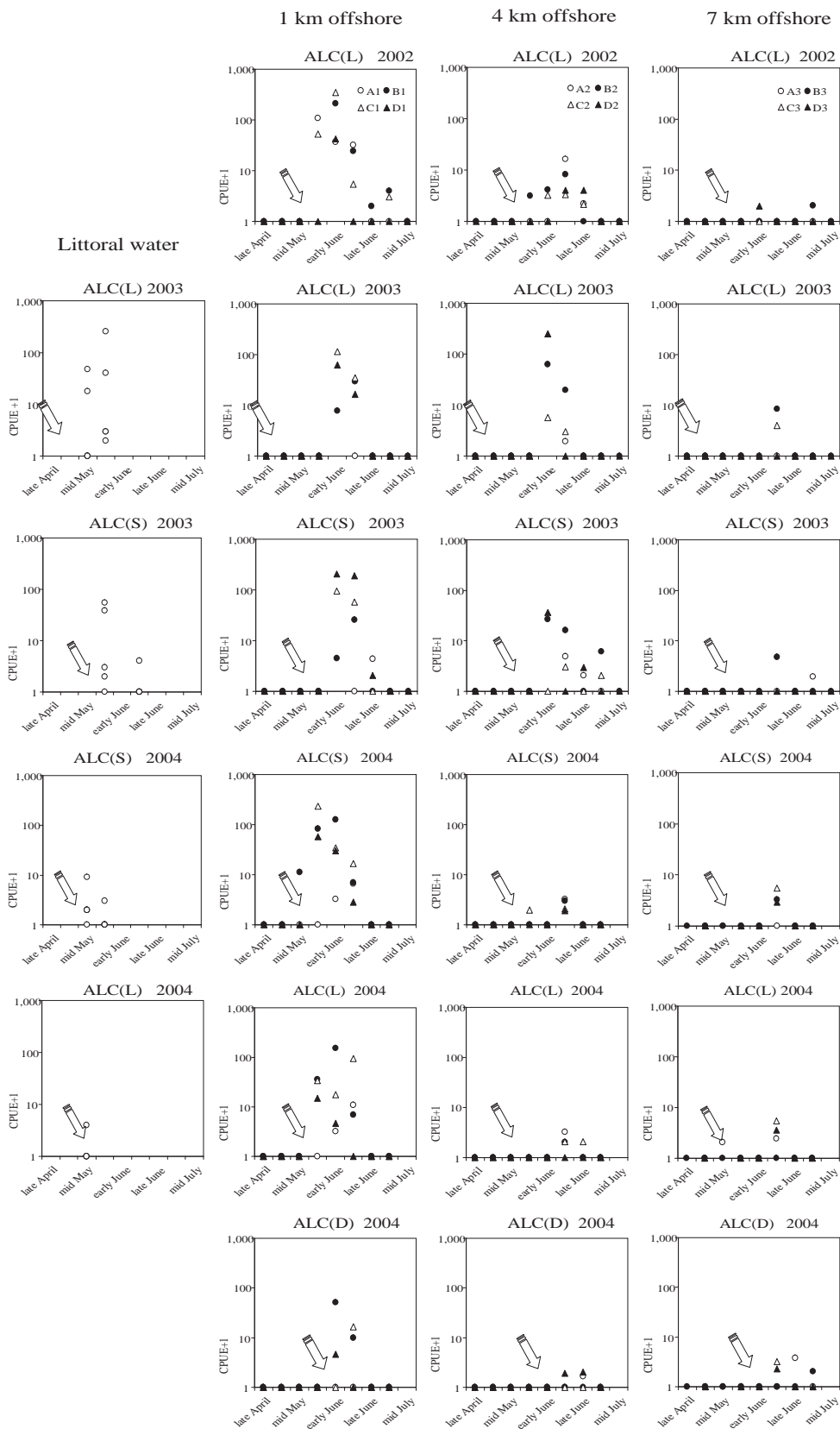
Fig. 4. Changes in CPUE (catch per unit effort, the number of juveniles per 2 km towing or per beach seine) of marked juvenile chum salmon captured at the littoral sites (beach seine), and at the 1-km, 4-km and 7-km offshore transects (trawl net) in the Okhotsk Sea from 2002 to 2004. Arrows indicate time of release.
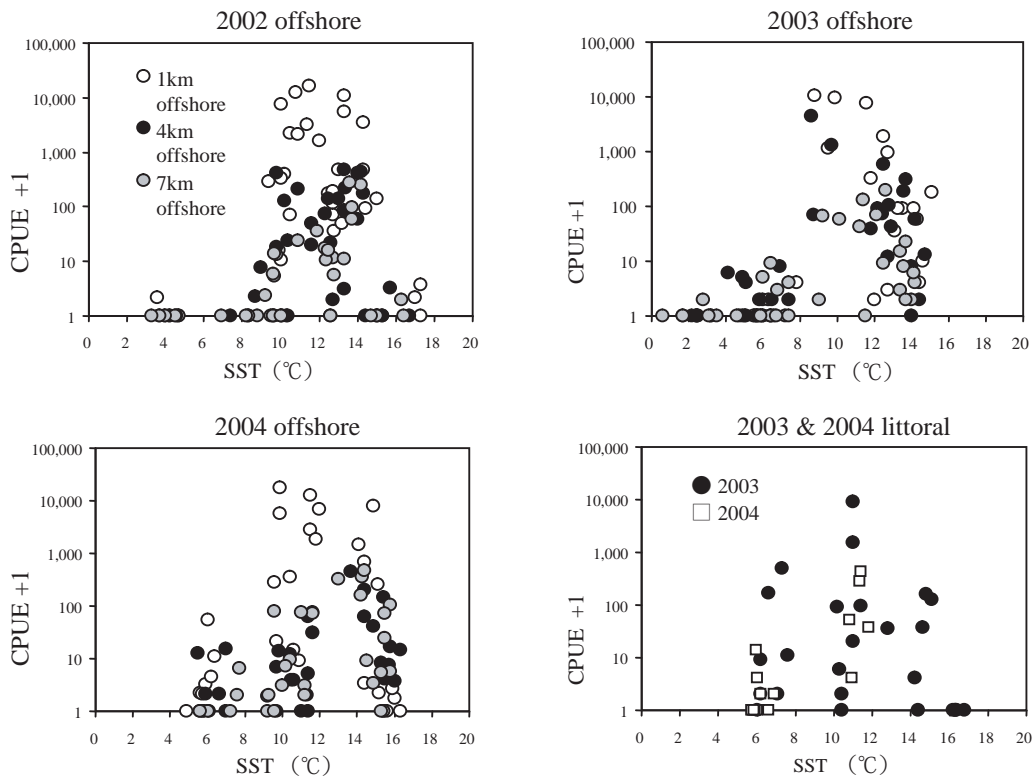
Fig. 5. Relationships between SST and CPUE in chum salmon including marked juveniles captured at the littoral sites (beach seine), and the 1-km, 4-km and 7-km offshore transects (trawl net) in the Okhotsk Sea from 2002 to 2004.
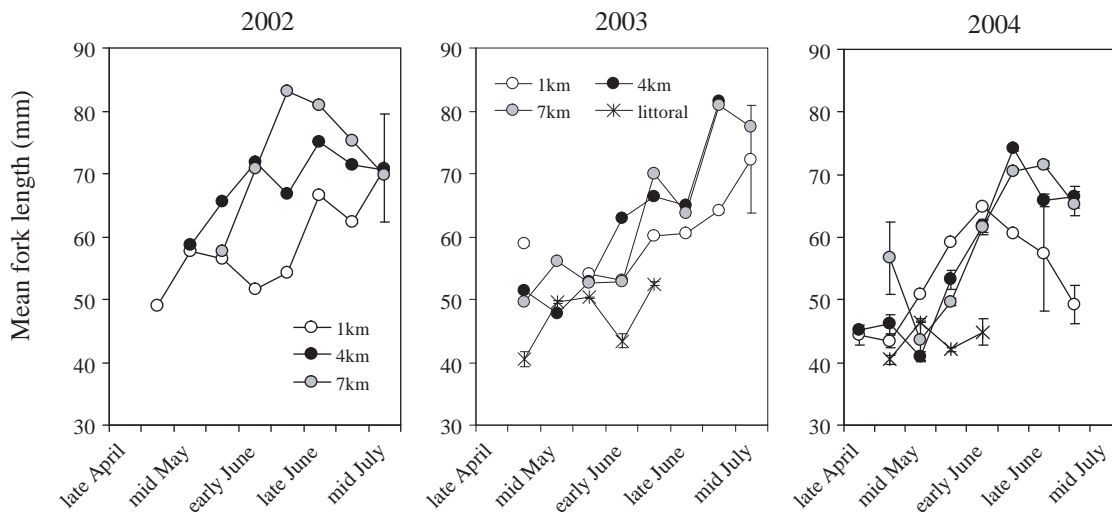

Fig. 6. Changes in mean fork length of unmarked juvenile chum salmon captured at the littoral sites, and the 1-km, 4-km and 7-km offshore transects in the Okhotsk Sea from 2002 to 2004. Bars indicate standard errors. Values not sharing a common small letter among years are significantly different at *p* < 0.05.

littoral zone was much lower than that in 2003. Unmarked juveniles in littoral waters were rarely caught after late June 2003 and mid June 2004, and had disappeared from coastal waters by mid July 2002 and 2003, and late June 2004.

Marked juveniles released in mid May 2002 and 2004 were first recaptured at the 1-km offshore transect in late and mid May, respectively (Fig. 4). In contrast, marked juveniles

released in mid May 2003 were not recaptured in coastal waters until early June when SSTs were > 8°C. Fish released in late April of the same year were recaptured in littoral areas in mid/late May. Marked chum rapidly disappeared from coastal waters after late June when SSTs were > 13°C, (e.g. marked juveniles released in late May 2004 remained in coastal waters for only three weeks).

Table 2. Specific growth rate (SGR) of each marked group captured 1 km off the coast (A1–D1) about 3 weeks after release from 2002 to 2004.

Year	ALC mark[*1]	At release		At recapture		Δ t	SGR[*2]
		Date	MFL (mm)	Date	MFL (mm)		
2002	L	May 17	46.62	June 6	52.94	20	0.0064
2003	L	April 28	47.46	May 22	53.69	24	0.0051[*3]
				June 4	59.20	37	0.0060
	S	May 15	47.48	June 4	53.80	20	0.0063
2004	S	May 16	47.95	June 8	59.33	23	0.0093
	L	May 16	46.79	June 8	57.26	23	0.0088
	D	May 30	47.90	June 17	55.94	18	0.0086

[*1] L, S and D represent single large ALC-banding, single small ALC-banding and double ALC-banding marks, respectively.
[*2] SGR = $(Ln(L_{t2}) - Ln(L_{t1})) / (t_2 - t_1)$, L_t is MFL (mean fork length).
[*3] SGR was computed using marked fry captured at the fishing seaport near B 1, because no samples were taken 1 km off the coast on May 22, 24 days after release. First capture was on June 4, 37 days after release.

Table 3. Specific growth rates as the slope of the exponential equation computed using individual fork length in marked groups captured after release from 2002 to 2004.

Year	ALC mark[*1]	At release		SGR (slop b, $L_t = a\,e^{bt}$)		
		Date	MFL (mm)	Littoral water	1 km offshore	4&7 km offshore
2002	L	May 17	46.62		[b]0.0058[D*2]	[a]0.0107[BC]
2003	L	April 28	47.46	0.0023	[b]0.0069[C]	[a]0.0078[D]
	S	May 15	47.48	0.0010	[b]0.0077[BC]	[a]0.0100[C]
2004	S	May 16	47.95	-0.0119	[b]0.0094[A]	[a]0.0124[A]
	L	May 16	46.79		[b]0.0090[AB]	[a]0.0116[AB]
	D	May 30	47.90		0.0090[ABCD]	0.0124[AB]

[*1] L, S and D represent single large ALC-banding, single small ALC-banding and double ALC-banding marks, respectively.
[*2] The values not sharing a common small letter between 1 km and 4&7 km offshore are significantly different. The values not sharing a common large letter among different groups in each offshore area are significantly different ($p < 0.05$).

Relationships between CPUEs and SSTs for both unmarked and marked juveniles in coastal waters were similar each year (Fig. 5). CPUEs were high when seawater temperatures ranged from 9 to 14°C, and sharply decreased below 9°C and above 14°C. In littoral waters, CPUEs were relatively high when temperatures were 6 to 14°C, peaking at 10°C.

Recapture rates (number of fish captured per one million released) in coastal waters varied between 131 and 957 (Table 1). The highest recapture rate (957) was recorded for L-marked juveniles released in mid May 2002, and the lowest (131) for D-marked juveniles released in late May 2004.

In the littoral waters, recapture rates in both 2003 and 2004 varied between 0 and 194.

Growth Rates

Mean fork lengths (MFL) of unmarked chum juveniles at the 1-km offshore transect in 2002 ranged between 50 and 60 mm until mid June, increasing gradually thereafter, reaching 70 mm in mid July (Fig. 6). In contrast, MFLs at the 4- and 7-km offshore transects increased sharply from mid to late May when CPUEs increased, reaching 75 mm and 80 mm in late June. As a result, there were significant differenc-

es in MFL between the 1-km and the 4- and 7-km offshore transects. In 2003, MFL of chum juveniles in each transect increased rapidly after early June when CPUEs increased. In 2004, MFL of juveniles at each transect increased rapidly after mid May (when CPUEs also increased), reaching 70–80 mm in mid June, except for those at the 1-km offshore transect. These data indicate that MFLs of juveniles in 2002 and 2004 under warmer conditions increased earlier than those in 2003 when temperatures were cooler. MFLs of chum captured in littoral waters were similar to or smaller than those at the offshore transects, and did not increase.

SGRs of marked juveniles during early periods (18 to 37 d after release) at the 1-km offshore transect where CPUEs were highest ranged from 0.0051 to 0.0093 (Table 2). SGRs for marked juveniles released in 2002 and 2003 varied between 0.0051 and 0.0064, lower than those (0.0086–0.0093) in 2004; in particular, SGR of juveniles released in late April 2003 was 0.0051 at 24 d post-release, and 0.0060 at 34 d post-release, lower than any others. Throughout the survey, SGRs of marked juveniles collected at the littoral sites in 2003 and 2004 were significantly lower than those in coastal waters (Table 3). SGRs for most fish caught at the 1-km

transect were highest in 2004. SGRs at the 4- and 7- km transects were significantly higher than those in littoral waters and at the 1-km offshore transect, indicating either that offshore chum grow fastest, or that larger chum move offshore. Although there were no significant differences in SGRs in 2003 between early (mid May) and late May released groups, MFL at the 1-km offshore transect were larger in the early released group (63–64 mm) than in the late released group (56 mm).

Stomach Contents

Mean stomach content indices (SCI, stomach content weight x 100 / body weight) for unmarked juvenile chum at the 1-km offshore transect were relatively high for the three years, except in 2002 when there was a decrease in June (Fig. 7). Although the SCI at the 4-km offshore transect were also relatively high, they decreased sharply in mid to late June. In contrast, SCI at the 7-km offshore transect were relatively high in June, especially in 2004. These changes in the composition of stomach contents were also observed in marked juveniles, except at the 7-km location where few samples
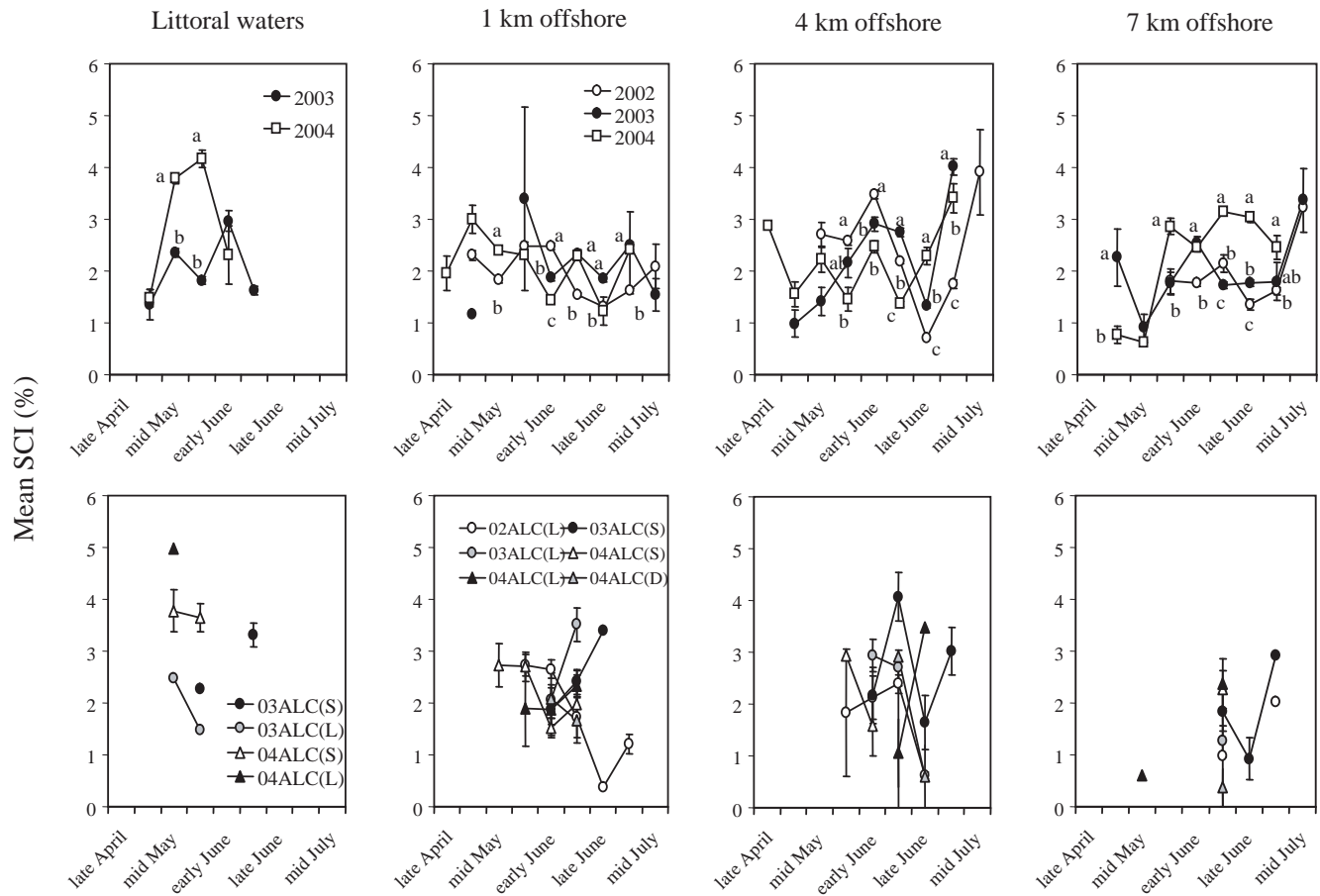

Fig. 7. Changes in mean values of stomach content indices (stomach content weight x 100 / body weight) of unmarked (top) and marked (bottom) juvenile chum salmon captured at the littoral sites and the 1-km, 4-km and 7-km offshore transects in the Okhotsk Sea from 2002 to 2004. Bars indicate standard errors. The values not sharing a common small letter among years (marked juveniles only) are significantly different at $p < 0.05$.

were taken. In littoral waters, SCI of juveniles with high CPUE in May 2003 were significantly lower than those in 2004 with lower CPUE.

Diet analysis of both unmarked and marked juveniles revealed that offshore juvenile chum in 2002 consumed primarily cold-water species of copepods (mainly small coastal species such as *Pseudocalaunus newmani* and large oceanic species such as *Neocalanus* spp.) and appendicularians (mainly *Fritillaria borealis* f. *typica*) in May, switching to warm-water small species such as cladocerans (mainly *Podon leuckarti* and *Evadne nordmanni*) and appendicularians (mainly *Oikopleura longicauda*) in June (Fig. 8). Beginning in late June, various amphipods, insects and fish eggs were consumed. Electivity indices showed that chum in 2002 favored cladocerans and appendicularians in June when SSTs were warm; copepods were not always preferred (Fig. 9). Juveniles in coastal waters in 2003 consumed predominantly cold-water copepods (mainly *Neocalaunus* spp.

and *Eurytemora herdmani,*) until May when CPUEs were very low. These were later replaced by warm-water species such as cladocerans (mainly *Podon leuckarti*) and appendicularians (mainly *Oikopleura longicauda*). Electivity indices showed that chum in 2003 initially favored copepods, but later switched to cladocerans and appendicularians. Diet composition of chum juveniles in the littoral zone in 2003 was different from that in coastal waters. Juveniles in the littoral zone consumed not only small pelagic copepods such as *P. newmani* but also small epibenthic crustaceans such as Harpacticoid copepods and amphipods, indicating that juvenile chum can change feeding behavior depending on nursery conditions. In 2004, the main diet at the offshore transects consisted of large copepods such as *Neocalanus* spp. After mid June when SSTs were warmer, feeding on copepods decreased, and more cladocerans, amphipods and fish eggs were added to the diet. Indices revealed that chum preferred copepods over cladocerans, unlike preferences in 2002 and
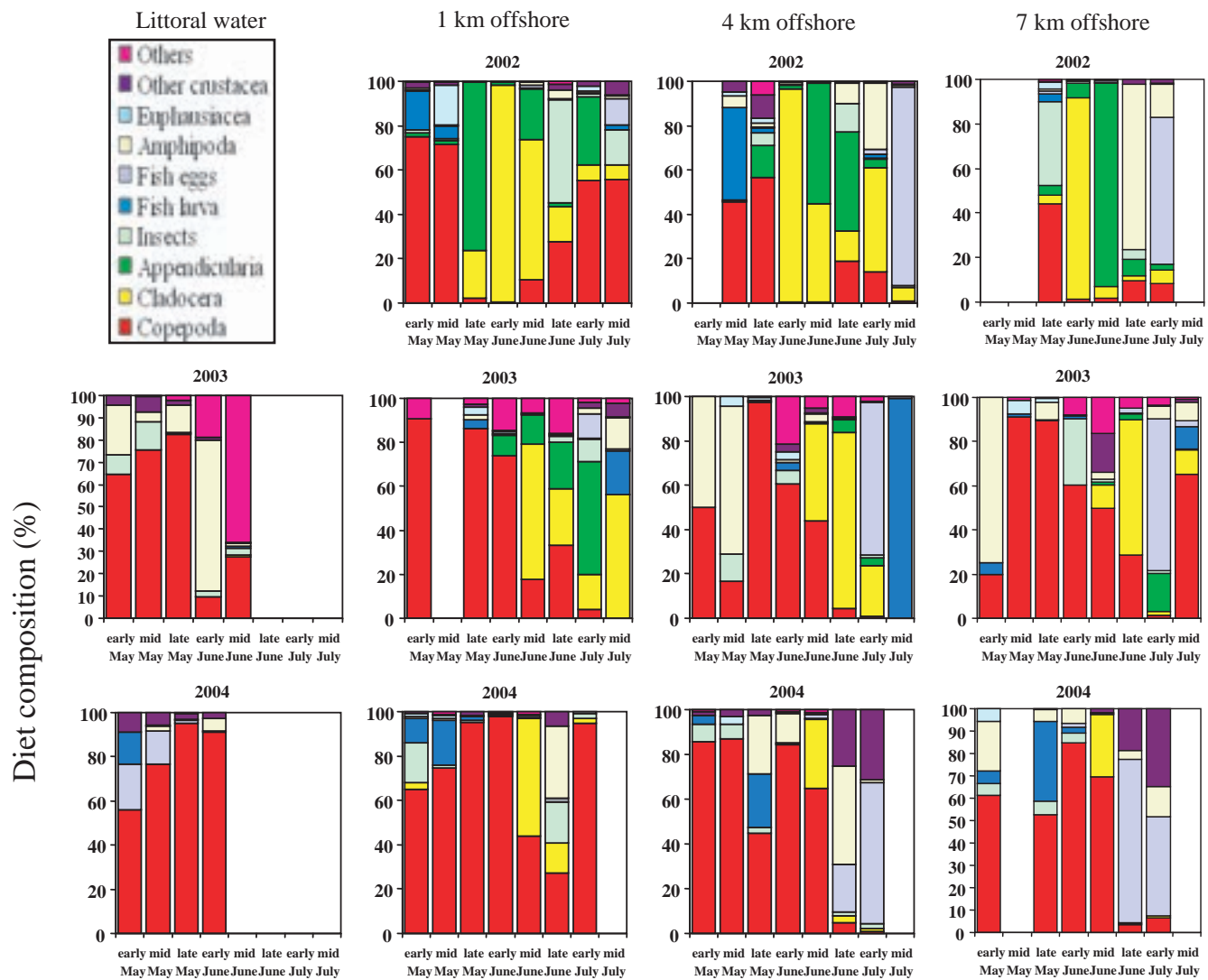

Fig. 8. Changes in diet composition (by number) including both unmarked and marked juvenile chum salmon at the littoral sites and the 1-km, 4-km and 7-km offshore transects in the Okhotsk Sea from 2002 to 2004.
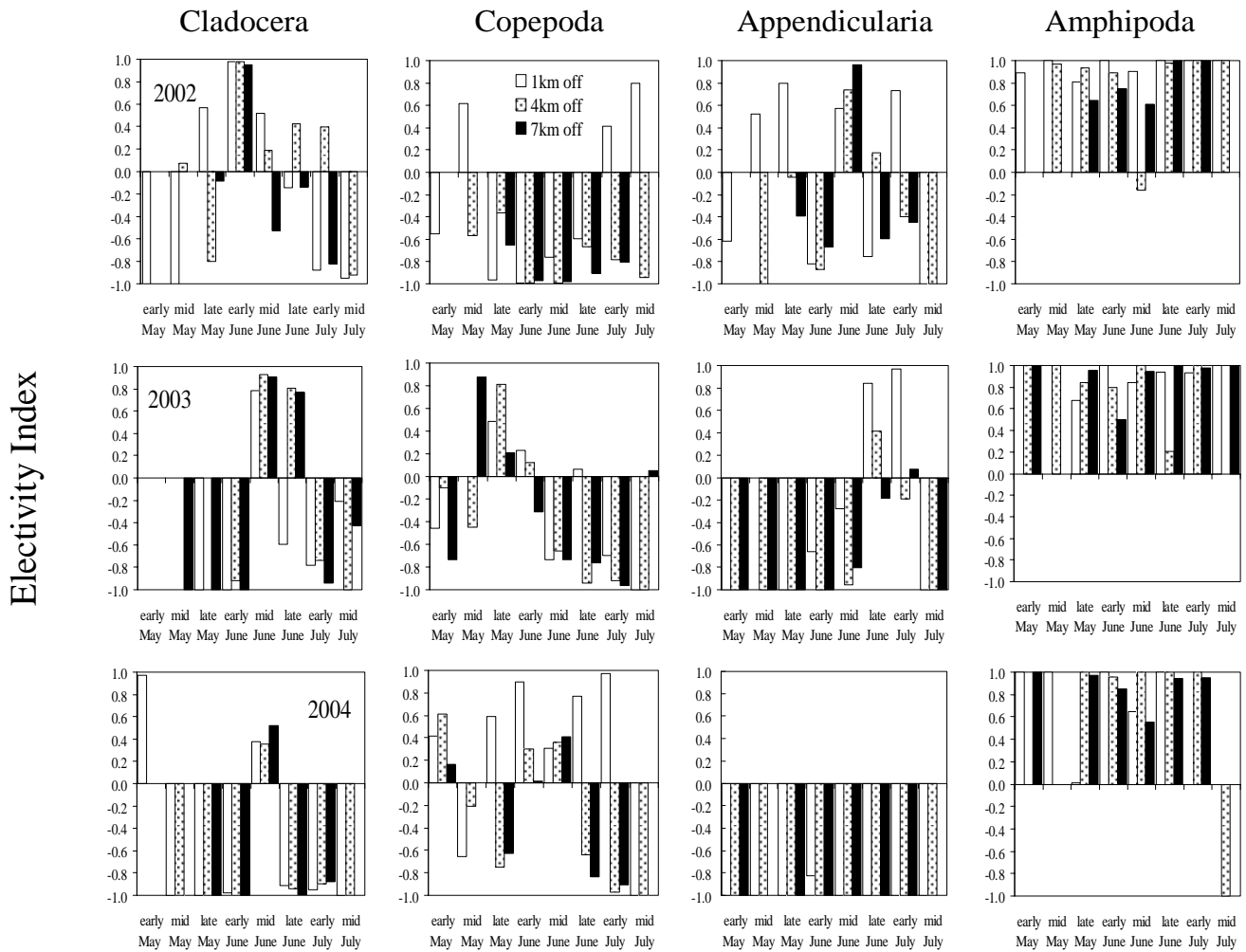
Fig. 9. Changes in electivity indices (by number) for four prey groups by juveniles including both unmarked and marked chum. Electivity (Jacobs, 1974): E = (ri - Pi) / (ri + Pi - 2ri · Pi); ri: % of i species in stomach contents; Pi: % of i species at the offshore transects. +1 = positive preference; -1 = negative preference.

2003. Amphipods (mainly *Themisto japonica*) were favored by chum throughout the season in 2002–2004. Diet at the littoral sites in 2004 differed from that in 2003, being dominated by pelagic copepods such as *Neocalanus* spp. and *E. herdmani*.

DISCUSSION

Although the Okhotsk Sea is usually covered with sea ice during the winter, the maximum coverage, and dates of arrival and disappearance varies year by year (Shimizu 2005). The sea ice disappeared in 2002 and 2004 in early March, one month earlier than in 2003 that saw the latest disappearance date in the past 10 years (Shimizu 2005; Asami et al. 2007). In 2003, the movement of the Soya Warm Current toward the Abashiri coast was delayed (Asami et al. 2007), allowing the cold Okhotsk Surface Water to occupy the study area longer. Consequently, SST in May 2003 ranged from 5.3 to 6.8°C,

much colder than in the warmer years 2002 and 2004.

Relatively high abundances of juvenile chum salmon were found in littoral waters and at the 1-km offshore transects from May to June each year. Lower abundances were recorded at the 4- and 7-km offshore transects. Fish were most abundant after May, and largest, at the transects farthest from shore. We conclude that the relatively large area extending from littoral waters to 1 km offshore are important nursery areas for chum juveniles. Juvenile chum are known to live in estuaries and littoral areas for long periods, and then move offshore as SSTs increase and fish grow larger (Kaeriyama 1986; Irie 1990). We found that chum salmon juveniles showed remarkable differences in spatial distribution year by year. In the warmer years, 2002 and 2004, when SST in the coastal waters exceeded 8°C in May, most unmarked chum juveniles were found near the 1-km offshore transect, not in littoral waters. This contrasts with the cooler year, 2003, when SST did not exceed 8°C in May. In 2003

chum remained either in littoral waters or at the fishing port for an extended period before moving 1 km offshore. These results suggest that coastal seawater temperatures may affect the behavior of chum juveniles soon after their seaward migration. This idea is strongly supported by the fact that marked juveniles released in late April 2003 were captured only in littoral waters or at the fishing port in May, and were first found in early June at the 1-km offshore transect. We suggest that juvenile chum salmon show two types of marine dispersal patterns that are influenced by SSTs. When offshore waters are < 8°C, many juvenile chum remain in littoral waters at 1–2 m depth or at the fishing port for extended periods. When offshore waters are > 8°C, many chum disperse rapidly to the 1-km offshore transect and remain there for a relatively long time before moving farther offshore.

These two temperature-related patterns affect growth and recapture rates. Marked juveniles in 2003 and 2004 grew poorly when they lived in littoral waters. Juveniles densely aggregated in littoral waters in 2003 fed poorly (lower SCIs) and consumed predominantly small epibenthic copepods, compared to the juveniles that were more widely dispersed in 2004. In addition, marked juveniles that moved 1 to 7 km offshore in 2003 generally grew more slowly than juveniles released in 2002 and 2004. It appears that when chum juveniles aggregate densely in the relatively narrow littoral and estuarine areas at colder temperatures, feeding and growth may be reduced due to shortages of food and/or low temperatures. This period of littoral or estuarine residence of chum juveniles may strongly affect early ocean survival.

The offshore movement of chum juveniles occurred from late June in 2004 to mid July in 2002 and 2003, coinciding with SST > 14–15°C and MFLs between 60 and 80 mm. Chum juveniles move offshore when SST, salinity and fish size exceed 13–14°C, 33.5–34.0 psu, and 70 mm FL, respectively (Mayama et al. 1982; Mayama 1985; Kaeriyama 1986; Irie 1990; Seki 2005). Our observations are consistent with previous research. Kaeriyama (1986) identified influences on offshore migration: an active migration to search for prey, and a passive migration arising from lack of food or escape from unsuitable environmental conditions such as high SST. Marked juveniles released in late May 2004 left coastal waters early despite a rapid growth rate because SSTs exceeded 14°C and prey abundance was low (Asami et al. 2007). In addition, recapture rates and fish sizes before moving offshore for late releases were less than those for early releases. These results support Kaeriyama's hypothesis. Recent survival for salmon returning to the Okhotsk Sea is known to be much lower in late-run chum than in early-run chum (Nagata et al. 2004). As hatchery juveniles from the late-run chum were released later (from late May to early June) they may have encountered unfavorable ocean conditions such as high SSTs and a shortage of prey during their shorter residence time in coastal waters. Therefore, recent low survival in the late-run chum might be the result of a mismatch in the timing of release of juveniles and environ-mental conditions in the ocean. Marked chum salmon released at different periods in 2002–2004 will return as 3- to 5-year-old adults from 2004 to 2009, which will allow us to test this hypothesis.

Optimal SST for releasing hatchery chum juveniles into Hokkaido rivers are between 5 and 13°C (Irie 1990; Mayama and Ishida 2003; Seki 2005). Seki and Shimizu (1996) discovered that return rates for chum juveniles released when coastal water temperatures were > 5°C were 0.216%, much higher than 0.056% when coastal water temperatures were < 5°C. But chum (46 mm FL) released at SST > 5°C were much larger than those (41 mm) released at SST < 5°C. Because mortality in chum salmon juveniles is strongly size-selective (Healey 1982), additional research is needed to conclude whether reduced return rates are caused by cooler temperatures (< 5°C). Some chum juveniles have been observed in coastal waters at 5°C (Irie 1990; Seki 2005), but most are found in coastal waters between 8 and 13°C (Kaeriyama 1986; Irie 1990; Seki 2005), which is consistent with our results. Therefore, it is reasonable to conclude that 5°C is unsuitable for chum juveniles.

Most marked chum salmon moved to the 1-km offshore transect within 10 d after release. Juvenile chum salmon in small streams are known to reach the ocean within 24 h (Iwata and Komatsu 1984; Nagata and Miyamoto 1986). Chum in larger (and longer) rivers reach the ocean within 10 d (Mayama et al. 1982). Therefore, we recommend that chum juveniles be released when coastal waters reach 7°C, enabling them to move rapidly to coastal waters

It seems reasonable that the upper SST limit for chum juveniles in coastal waters is 13°C; other researchers (Kaeriyama 1986; Irie 1990; Kawamura et al. 2000; Seki 2005) report catching no fish in coastal waters exceeding 14°C. Fish that are 70 mm FL and 3 g BW are thought to have the potential to move actively offshore, based on ecological conditions, and physiological and morphological characteristics (Kaeriyama 1986; Irie 1990). High growth rates of marked juveniles were recorded in 2004 when their diet was dominated by large cold-water copepods such as *Neocalanus* spp. *Neocalanus* build a substantial high-energy lipid reserve which is utilized during the subsequent winter for egg development (Cooney 1986). A recent study (Seki, 2005) showed that cold-water zooplankton abundance peaks at 10°C, and then declines rapidly as temperatures increase. At the Abashiri coast, a high abundance of cold-water zooplankton, especially large copepods, was also observed at temperatures below 10°C (Asami et al. 2007). Releases of chum salmon when SST reaches 13°C may be too late to best utilize cold-water copepods. We suggest that the optimal upper SST limit in coastal waters for releasing juvenile chum should be < 11°C. In summary, one should avoid releasing juvenile chum salmon when coastal water temperatures are either < 7°C or > 11°C.

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A Shift in Pink Salmon Dominance in the Okhotsk Sea of Hokkaido in Relation to Coastal Environments during Early Sea Life

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Abstract: Although dominance by the even-year line of pink salmon in the Okhotsk Sea of Hokkaido was maintained from the 1990 to 2000 brood-years, a shift back to odd-numbered year returns occurred. We have monitored the distribution of juvenile pink salmon and the ocean environment in the Abashiri coastal waters of the Okhotsk Sea since 2002 when juveniles from 2001 brood-year pink salmon went to sea. SST measurements were much higher when odd-year juveniles entered coastal waters in 2002 (8.2–9.7ºC) and 2004 (5.5–12.0ºC) than when even-year juveniles entered coastal waters in 2003 (5.3–6.8ºC). Pink salmon juveniles were widely distributed along the coast in May 2002 and 2004, while juveniles in 2003 were densely distributed and restricted to the littoral zone. Mean fork length in 2003 was significantly smaller than those in the other two years. The final number of juveniles captured along the coast from May to July 2003 was 4,700, much lower than the numbers caught in the other two years (19,200 and 21,900, respectively). More interestingly, the abundance of adults in 2003 from pink juveniles (2001 brood year) that experienced the warm temperatures in 2002 was much higher than adults in 2004 that had experienced the cooler temperatures in 2003, resulting in the shift in dominance. These results suggest that shifting between dominance lines might be caused by thermal conditions in coastal waters that result in either long estuary residence times with larger aggregations of fish or rapid dispersal with wider occupation of nursery grounds by pink salmon juveniles after seaward migration.

Keywords: pink salmon, two-year cycle, dominance shift, early sea life, SST, estuary residence

INTRODUCTION

Pink salmon (*Oncorhynchus gorbuscha*) occur mainly in eastern Hokkaido, especially in the Okhotsk Sea. Numbers of pink salmon were low from the 1970s to the 1980s with a two-year cycle of dominance in odd-numbered years. However, in the early 1990s the population size increased sharply, especially in even years, exceeding 10 million. Subsequently, a shift from odd- to even-year dominance occurred (Nagata and Kaeriyama 2004). More interestingly, a shift back to dominance in odd-numbered years has occurred recently.

A great difference in population size between even and odd years is well known in the North Pacific Ocean (Heard 1991). This two-year cycle dominance tends to persist because pink salmon have a two-year life cycle. Although the most probable cause of the initial disparity between two lines is either a disastrous decrease (or a dramatic increase) in the survival rate of one line over the other (Neave 1953; Ricker 1962), little information has been collected to clarify the mechanism that causes the shift in the dominant year. It has been assumed that high mortality of salmonids often occurs

soon after juveniles or smolts enter the ocean (Bax 1983; Pearcy 1992; Mueter et al. 2002). The survival rate for pink salmon, especially, may be influenced by mortality during early sea life rather than by environmental factors during downstream migration (Manzer and Shepard 1962; Parker 1965, 1968; Healey 1991; Willette et al. 2001), such as prey availability, feeding condition, zooplankton density and timing of the zooplankton bloom (Healey 1980, 1991; Willette 2001; Willette et al. 2001). Therefore, high mortality or survival during early sea life may cause the shift in pink salmon dominance.

We have monitored the distribution of juvenile pink and chum salmon (*O. keta*) and the ocean environment in the Abashiri coastal waters of the Okhotsk Sea since 2002 when the 2001 brood-year fish entered the sea as juveniles (Nagata et al. 2004, 2005; Ando et al. 2005; Asami et al. 2005). In 2003, a shift back to dominance in odd-numbered years occurred. In this paper we propose a hypothesis that the shift from even- to odd-year dominance in recent years might be caused by differences in growth and habitat conditions in coastal waters during the early sea life of pink salmon.

MATERIALS AND METHODS

Population Structure of Pink Salmon in Okhotsk Sea of Hokkaido

In order to investigate status of pink salmon and the shift in dominance in the Okhotsk Sea of Hokkaido, data on commercial catches and escapement were analyzed. Annual data on commercial catches in the Okhotsk coastal waters from Cape Soya to the tip of the Shiretoko Peninsula were collected by staff of the Hokkaido Fish Hatchery in collaboration with the local fisheries cooperatives. Escapement data were collected in the 14–26 rivers where salmon enhancement programs and hatcheries operate weirs. We calculated the spawer-to-recruit (SR) index showing survival rates that normalized the data and removed possible within-stock, density-dependent effects (Peterman et al. 1998). This index was the time series of brood-year residuals (i.e., anomalies) from a Ricker (1954) stock-recruitment model. We used available data for odd-year and even-year lines to fit a Ricker model by linear regression of *Ln* (recruit per spawner) on spawner abundance and then calculated SR values as deviations from the line (Peterman et al. 1998).

Sampling Survey and Biological Analysis

Twelve study sites were established in Abashiri coastal waters (Fig. 1). Four sites (A1–D1) were set up 1 km offshore. Four study sites were also established at 4 km (A2–D2) and 7 km (A3–D3) offshore, respectively. The depths at the study sites were 10–15 m at 1 km offshore, 20–30 m at 4 km offshore and 30–40 m at 7 km offshore. Pink juveniles were collected with a surface trawl net (8 m wide x 5 m deep mouth, 18 m long, with wing nets 7 m long and a central bag with 5 mm mesh). The trawl was towed along each transect in the 1 to 2 m surface layer for 1–2 km at 4–6 km/h during the day (5:00–14:00) at 10-d intervals from late April to early July 2004 and mid July 2002 and 2003. Several sites were not sampled because of adverse weather conditions. One study site at the Abashiri fishing port was established in late May 2003. The trawl net was towed there for 0.5 km to capture fish. Another study site was set up in the littoral zone. Pink salmon juveniles were captured using a beach seine (3.5 m wide x 2 m deep mouth, 10 m long, with wing nets 3 m long and a central bag with 3 mm mesh) from 2002 (late May only) to 2004.

Captured fish were sacrificed with an overdose of MS 222 to prevent regurgitation and defecation, and preserved in 5% neutralized freshwater formalin. They were transferred to 70% ethanol after 12 to 24 h. When large numbers of fish were captured, random samples were preserved and the remainder were released soon after weights were obtained to estimate the total number of fish captured. CPUE in surface trawl nets was computed as the number of pink salmon juveniles caught after 2 km towing because of differences in towing distances among study sites. CPUE in beach seines used the actual number of pink salmon juveniles caught because there was little difference in the towing distances between sites. Sea surface temperature (SST) and salinity (SSS) at each study site were measured with STD.

Because chum salmon juveniles were also captured, pink salmon were distinguished from chum by parr marks and pigmentation of the tail against a white background (Phillips 1977; Shirahata 1981). If these characteristics were not evident, gill rakers were counted, because pink salmon have more gill rakers than chum salmon of similar size (Okada and Nishiyama 1970; Shirahata 1981). Pink salmon juveniles at each study site were measured for fork length and wet body weight, to the nearest 1 mm and 0.01 g, respectively. Stomachs in juveniles were dissected and weighed to the nearest 0.0001 g. After the contents were removed, the empty stomachs were re-measured to calculate the weight of stomach contents. A stomach content index (SCI) was calculated by the following formula: SCI (%) = (weight of stomach contents) / (body weight) x 100. Prey items were identified according to taxonomic categories using a binocular microscope.

Statistical Analysis

Differences in fork length and SCI after arcsin square-root transformation of data on juvenile pink salmon captured from the littoral area, and the 1 km, 4 km, and 7 km off-
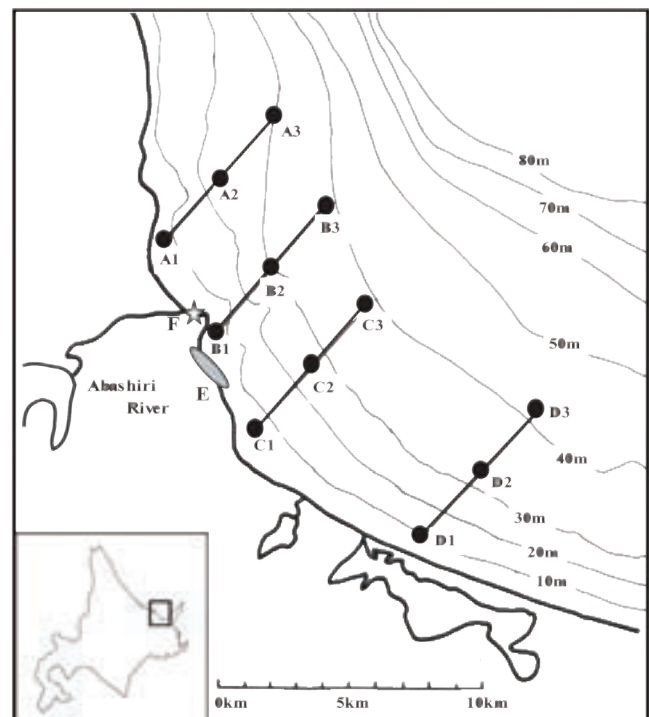

Fig. 1. Map showing the study sites at the fishing port (F), littoral areas (E), and 1 km, 4 km and 7 km off the Abashiri coast (A–D) in the Okhotsk Sea.
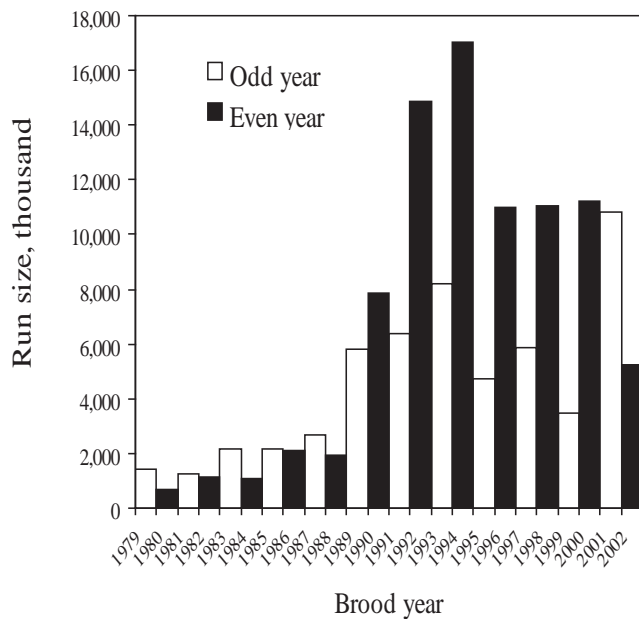
Fig. 2. Population size based on commercial catches and escapement of pink salmon in the Okhotsk Sea of Hokkaido since the 1979 brood year.

Fig. 3. Relationships between commercial catch and escapement of pink salmon in the Okhotsk Sea of Hokkaido since the 1979 brood year.

shore transects in the same year or among three years were compared with a one-way analysis of variance (ANOVA, $p = 0.05$). If a significant difference was found, a multiple comparison between them was carried out using Scheffe's test (Zar 1984). Data for each offshore transect consisted of information from all 4 sites (A, B, C and D).

Modes of spatial distribution for juvenile pink salmon in the coastal waters were analyzed using I_δ (Morisita 1959). $I_\delta = (\Sigma \, _i^N = 1 n i \, (n i - 1)) \, N / n \, (n - 1)$ where N is the number of samples, ni is the number of individuals in the ith sample, and n is the total number of individuals in all the samples. If I_δ equals 1, the dispersion of individuals is random; if > 1, the individuals are aggregated; and if < 1, the population has a regular pattern. The significance of the deviation from 1 is tested by the statistic F, where $F = (I_\delta \, (n - 1) + N - 1)/(N - 1)$ (Poole 1974).

Electivity indices (E) for food preference were calculated from the formula of Jacobs (1974): $E = (ri - pi) / (ri + pi - 2ripi)$ where ri is the proportion of i prey animal consumed by fish and pi is the proportion of the i animal available at the study site. Electivity ranged from -1 to +1; -1 indicates the strongest negative preference and +1 the strongest positive preference. Zooplankton data reported by Asami et al. (2007) were used for analysis.

RESULTS

Pink Salmon Population Structure

Population sizes of pink salmon in the Okhotsk Sea of Hokkaido remained low from 1970s to 1980s (Fig. 2), showing dominance in odd-numbered years. In the early 1990s,
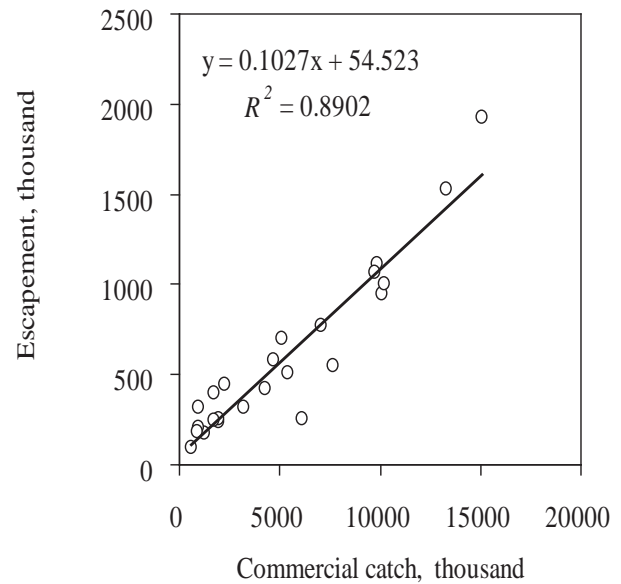
population sizes increased sharply (often exceeding 10 million fish), especially in even years. After that a shift from odd- to even-year dominance occurred. While even-year dominance was maintained from the 1990 to 2000 brood year, a shift back to odd-numbered year dominance occurred beginning with the 2001 brood year. The relationship between commercial catch and escapement was positively correlated (Fig. 3), strongly suggesting that pink salmon captured by commercial fishing originated from strains that reproduce in the rivers flowing into the Okhotsk Sea of Hokkaido.

The highest SR index in even-years was recorded in the 1990 brood year when even-numbered year populations dominated. After that, SR values decreased gradually eventually reaching the lowest level in the 2002 brood year (Fig. 4). In contrast the SR indices suddenly skyrocketed in the 2001 brood year when dominance shifted to odd-numbered years, although SR indices in odd years were also relatively high from 1989 to 1993, then decreasing until the 2001 brood year. These results suggest that survival of pink salmon in the 2001 brood year was high and survival in the 2002 brood year was low.

SST and SSS in Coastal Waters

Although the mean SST at each offshore transect in late April in 2002 was $< 5°C$, it rapidly increased, exceeding $8°C$ in early May, and then increased further in June, eventually reaching $14–15°C$ in mid July when our investigation was completed (Fig. 5). On the other hand, mean SST in 2003 was colder than in 2002 until mid June. In 2003 while mean SST at the 1 km offshore transect in late April was $4°C$ the same as in 2002, the mean SST at the 4 and 7 km offshore
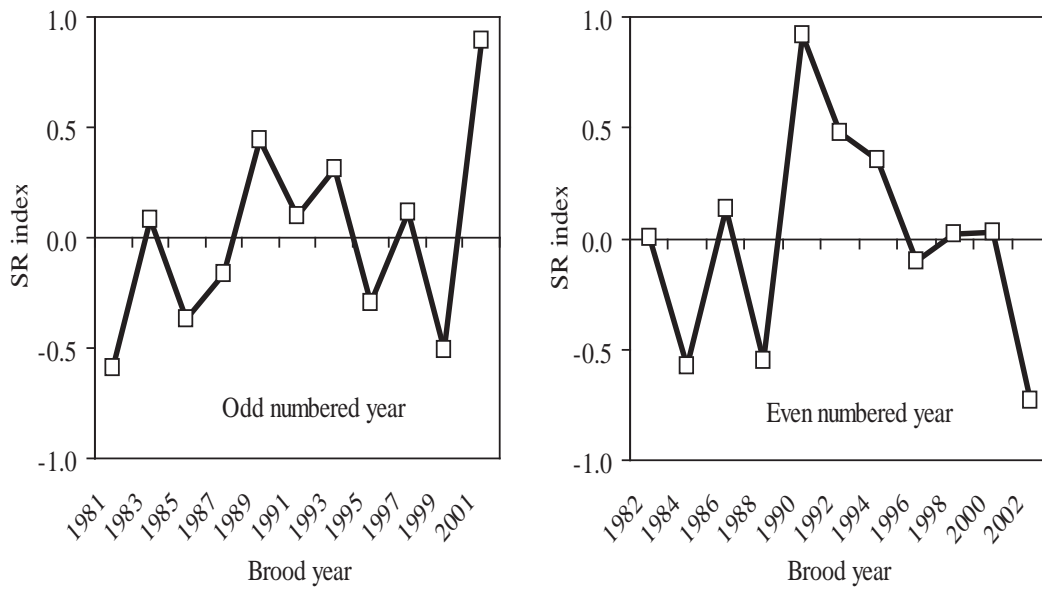
Fig. 4. Time series of spawner-to-recruit (SR) indices for pink salmon in odd- and even-numbered years in the Okhotsk Sea of Hokkaido. SR indices are residuals from the best-fit Ricker (1962) model.
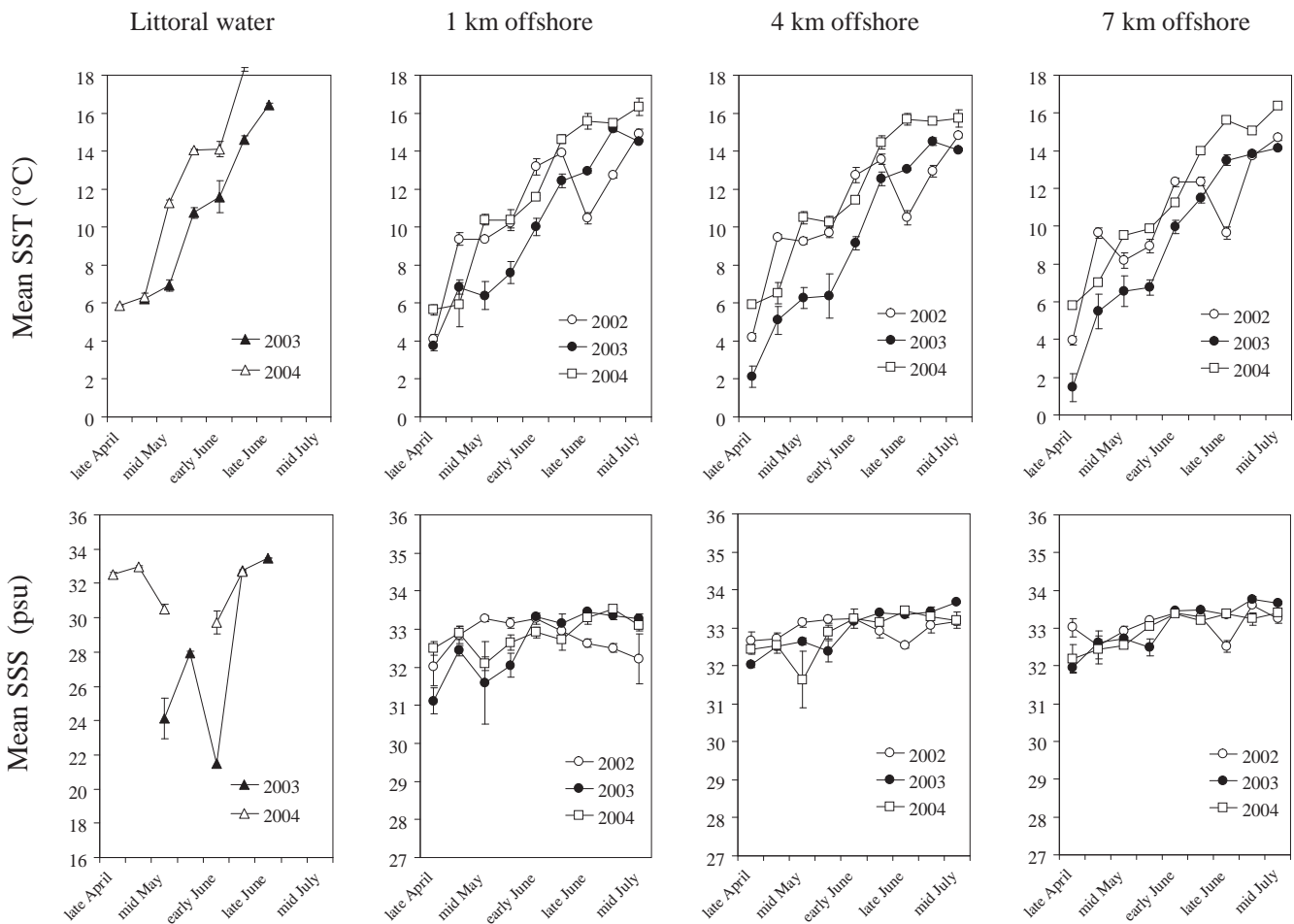

Fig. 5. Changes in mean values (with S.E.) of SST and SSS at the littoral site, and the 1 km, 4 km and 7 km transects off the Abashiri coast in the Okhotsk Sea from 2002 to 2004.
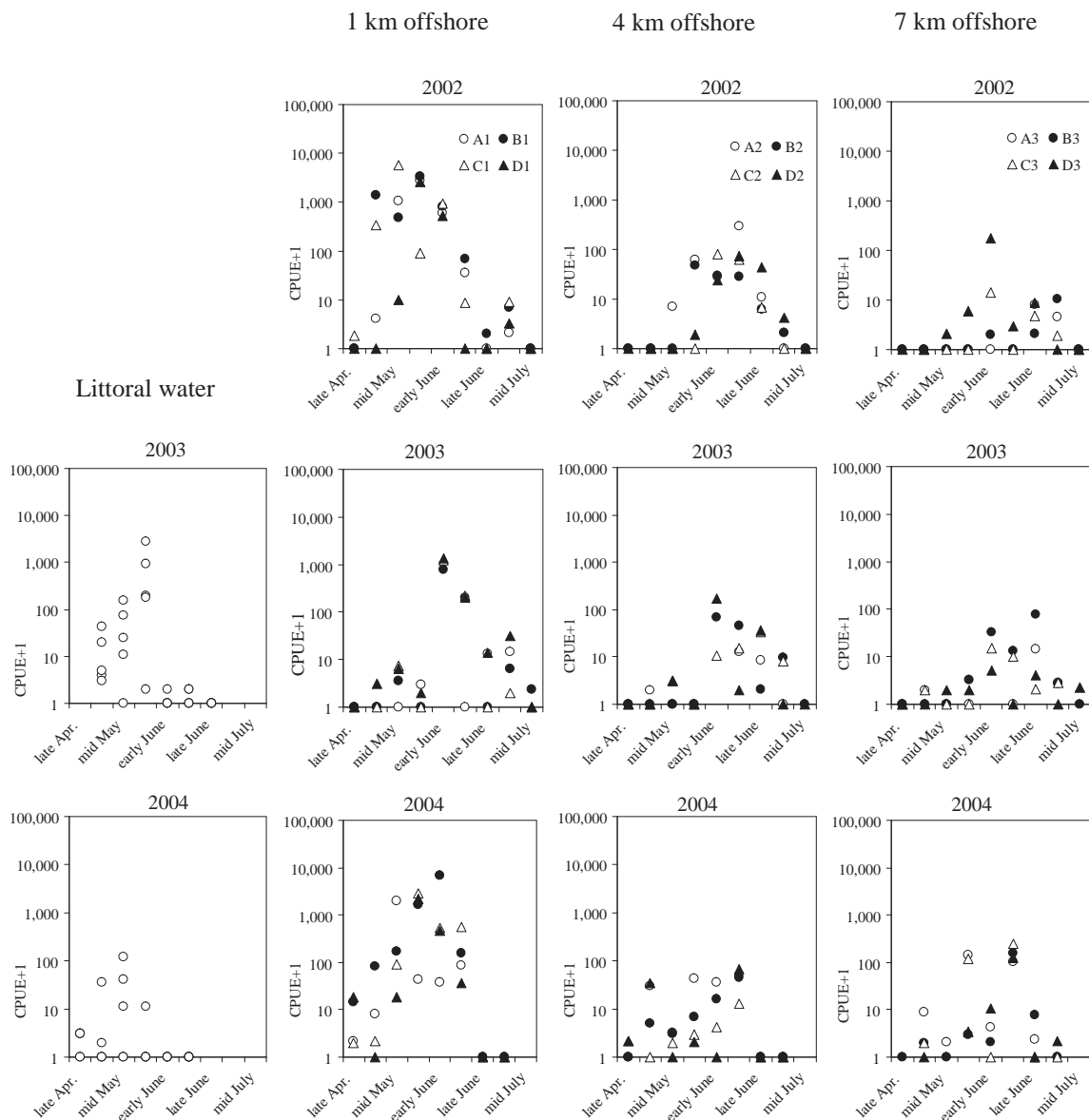
1 km offshore   4 km offshore   7 km offshore

Littoral water

Fig. 6. Changes in CPUE (catch per unit effort, the number of juveniles per 2 km towing or per individual beach seine) of juvenile pink salmon captured at the littoral site (beach seine), and the 1 km, 4 km and 7 km transects (trawl net) off the Abashiri coast in the Okhotsk Sea from 2002 to 2004.

transects was 2°C, much colder than in 2002 and 2004. By early May, mean SST in 2003 increased at every study site, but still remained below 8°C. By early June 2003 mean SST exceeded 8°C at every study site in offshore coastal waters, eventually reaching 14°C in July, similar to 2002. In 2004, the increasing trend in mean SST was almost the same as in 2002 except for colder temperatures in early May and warmer temperatures in mid to late June (Fig. 5).

Although only one set of data on SST was collected in 2002 in the littoral area, by late May, the mean SST there had already reached 14°C, almost the same as in 2004, and warmer than in the coastal waters at the same time in 2002 (Fig. 5). In 2003, mean SST at the littoral site gradually increased from 6 to 7°C from late April to mid May, and

exceeded 10°C by late May, differing from coastal waters where temperatures were below 8°C in the same year. Mean SST at the littoral site increased in 2003, reaching 16°C in late June, 3°C warmer than coastal waters. Although mean SST in 2004 was the same as in 2003 until early May, temperatures exceeded 11°C in mid May, 5°C warmer than in 2003, eventually reaching18°C in mid June.

Mean SSS along the 1 km offshore transect from late April to late May 2003 varied between 31 to 32.5 psu and was lower than in the other two years. Mean SSS at the 1 km transect in 2002 gradually decreased from 33 to 32 psu differing from values in 2003 and 2004 which remained over 33 psu (Fig. 5). There were almost no differences in salinity at the 4 and 7 km offshore transects between years, increasing

from 32–32.5 to 33–33.5 psu from late April to mid July.

Juvenile Pink Salmon Distribution

The total number of juveniles captured along the coast in 2003 was estimated to be 4,684 fish, much lower than the numbers caught in the other two years (21,867 in 2002 and 19,167 in 2004). In contrast, the total number of juveniles collected in the littoral area in 2003 was estimated to be 4425 fish, much higher than the 222 fish collected in 2004. Moreover, great differences were seen in the spatial distribution of juvenile pink salmon in littoral and coastal waters during the three years of this study.

In 2002 during warm conditions in May, CPUEs at all sites along the 1 km transect were relatively high in early May, and reached a peak in mid to late May (Fig. 6). By mid June, CPUEs decreased rapidly to < 100 fish at each site along the 1 km offshore transect. In contrast, CPUEs at the 4 km and 7 km offshore locations were much lower than those at the 1 km offshore site throughout the survey, with peak CPUEs along both transects occurring 10 days later. Although beach seinings in 2002 were carried out only in late May, no pink salmon juveniles were captured. The Morisita I_δ from early to mid May 2002 was very high (> 7), and then rapidly decreased to 2–3 along with a decrease in CPUE at the 1 km offshore transect and an increase at the 4 and 7 km offshore transects (Table 1). These results indicated that juvenile pink salmon after seaward migration in 2002 were densely aggregated at the 1 km offshore location early in the season, and soon afterward dispersed to the 4 and 7 km offshore sites.

In 2003 under cooler sea water temperatures in May, CPUEs at the 1 km offshore site were relatively low (< 10 fish in May) suggesting that few fish were there. More interestingly, CPUEs at the 1 km offshore sites in 2003 suddenly reached a peak in early June, about one month later than in 2002, but at much lower CPUEs than in 2002. The appearance of pink salmon juveniles at the 4 and 7 km offshore locations was also delayed in 2003. The relatively low I_δ (< 4)

Table 1. Changes in Morishita I_δ of pink salmon juveniles captured in coastal waters.

	2002	2003	2004
Late April	10.00[NS]*	-	3.72
Early May	8.17	1.33[NS]	3.78
Mid May	7.72	2.20	9.32
Late May	3.87	1.71[NS]	3.79
Early June	2.55	3.56	8.96
Mid June	3.76	3.09	2.06
Late June	3.47	2.67	8.16
Early July	1.80	2.81	12.00[NS]
Mid July	-	2.31	-

*NS indicates that the value of the Morishita index was not significantly different from "1", showing random distribution.

was maintained from May to July indicating that pink salmon juveniles were distributed more evenly in coastal waters in 2003 than in 2002. In the littoral waters, pink salmon juveniles in May were more abundant than in the coastal waters, especially in late May when CPUEs were highest. Although surface trawling at the fishing port was carried out only in late May, 302 pink salmon juveniles were captured. By early June, most pink salmon juveniles suddenly disappeared from littoral waters. These results suggest that most of juvenile pink salmon after seaward migration in 2003 remained in the littoral waters and at the fishing port for a long time without moving to the 1 km offshore transect. However, by early June with SST > 8°C they dispersed more evenly into the coastal waters, differing somewhat from the 2002 event. However, the timing of the dispersal of juveniles to coastal waters was almost the same in 2003 as in 2002 (Fig. 6).

In 2004 with warm seawater temperatures in May, similar to the 2002 event, a few pink salmon appeared at the 1 km offshore transect in late April, with numbers increasing gradually thereafter. The peak CPUE at the 1 km offshore transect occurred between late May and early June, 10 days later than in 2002, but 20 days earlier than in 2003. CPUE at the 4 and 7 km offshore transects were low in early May, and then increased from late May to mid June. Pink salmon juveniles in the coastal waters suddenly disappeared in late June. The I_δ was varied in 2004 with alternating high (8) and low (2–3) values, indicating that aggregations at the 1 km offshore transect and dispersion to the 4 and 7 km offshore transect occurred repeatedly. While pink salmon juveniles appeared in littoral waters in early May in 2004, similar to 2003, the peak occurrence was 10 days earlier than in 2003 and maximum CPUEs were much lower. Therefore, while some pink salmon (after downstream migration) in 2004, as well as 2003, spent time in littoral waters, most pink salmon juveniles moved rapidly to the 1 km offshore transect in the warmer year (2004) and remained there until mid June with some dispersal to the 4 and 7 km offshore transects (Fig. 6).

Relationships between CPUE and SST in coastal waters showed almost the same pattern in all three years (Fig. 7). The high CPUEs were observed at seawater temperatures between 9 and 14°C. CPUEs sharply decreased when temperatures were < 9°C and > 14°C. In the littoral waters, relatively high CPUEs occurred at 6 to 14°C with a peak at 10°C.

Pink Salmon Size Structure and Growth

Length-frequency distributions of pink salmon from each time period at the 1 km, 4 km and 7 km offshore transects in the three years and in littoral waters in two years were mostly unimodal except for some data showing skewed distributions. Assuming that mean fork lengths of pink salmon pooled at each offshore transect or in littoral waters were representative of pink salmon juveniles at each location, these mean values were statistically compared among years
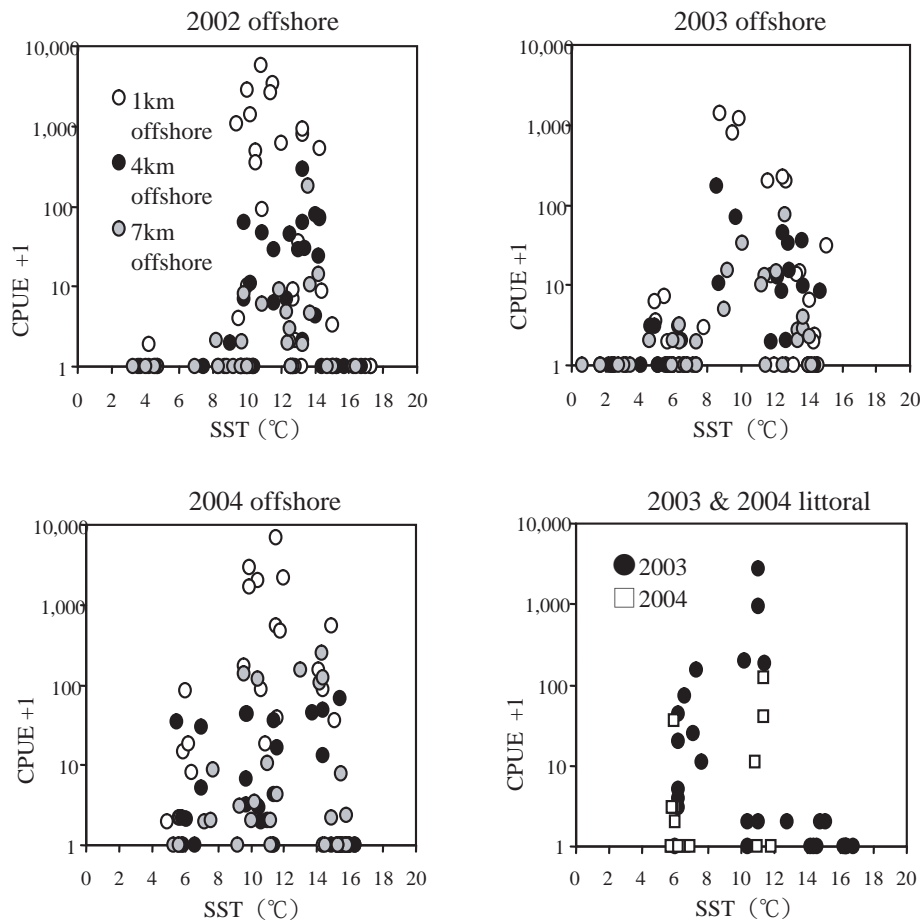
Fig. 7. Relationships between SST and CPUE in pink salmon juveniles captured at the littoral site (beach seine), and the 1 km, 4 km and 7 km transects (trawl net) off the Abashiri coast in the Okhotsk Sea from 2002 to 2004.

and locations.

When comparing mean fork length (MFL) among locations, different trends were found in the same year or among different years (Fig. 8). While MFL at the 1 km offshore transect in 2002 increased linearly from 46.3 mm in early May to 72.9 mm in early July, MFLs from the 4 km and 7 km transects increased more rapidly after mid May, and eventually became significantly larger than juveniles from the 1 km transect, except for early July. In contrast, MFLs at all locations in 2003 did not increase until late May but thereafter increased rapidly, although MFLs of juveniles at the 4 and 7 km transects were significantly larger than those from the 1 km transect from late June to early July. In 2004 while MFLs also showed no increasing trend until mid May, thereafter MFLs at every location increased rapidly, similar to 2003. Although MFLs at the 1 km offshore transect was larger than at the 4 km and 7 km transects in late May 2004, this difference disappeared in early June and eventually MFLs at the 7 km transect became significantly larger than others in mid June.

When comparing MFLs among years at the same location, different trends were observed in the three years (Fig. 8). While MFLs at the 1 km offshore transect from early

to mid May 2004 were significantly smaller than those in 2002, MFLs in late May 2004 increased to 54.5 mm as large as in 2002. Eventually MFLs in early and mid June 2004 were significantly the largest. In contrast, while MFL at the 1 km offshore transect in 2003 was 45.5 mm in early May as large as in 2002, MFLs decreased to 36.4 mm in late May, significantly smaller than those in the other two years. MFL in early June 2003, when pink salmon were very abundant at the 1 km transect, was 49.4 mm, significantly smaller than in other years (58.8 mm in 2002 and 64.4 mm in 2004). These MFLs recovered to 61.8 mm by mid June, similar to the other transects. At the 4 km transect, MFLs in 2002 were significantly larger than in 2003 and 2004 from late May to late June. There were no significant differences between 2003 and 2004 except for early June pink salmon were very abundant at the 1 km transect. At the 7 km transect, MFLs in 2002 were always significantly the largest from late May to late June. In contrast, MFLs in 2003 were always the smallest except for early July when few pink salmon were seen. There were no significant differences in MFLs of juveniles in littoral waters between 2003 and 2004. These results suggest that pink salmon juveniles in 2002 and 2004 grew more rapidly than in 2003, and this tendency became more obvi-
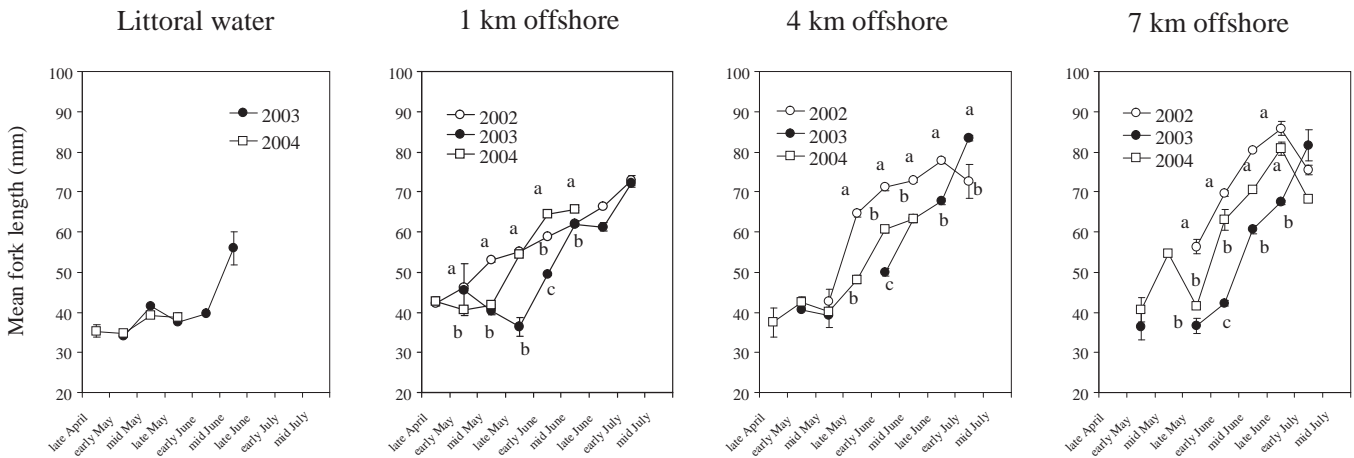
Fig. 8. Changes in mean fork length (with S.E.) of juvenile pink salmon captured at the littoral site, and the 1 km, 4 km and 7 km transects off the Abashiri coast in the Okhotsk Sea from 2002 to 2004. Values not sharing a common small letter among years are significantly different at *p* < 0.05.
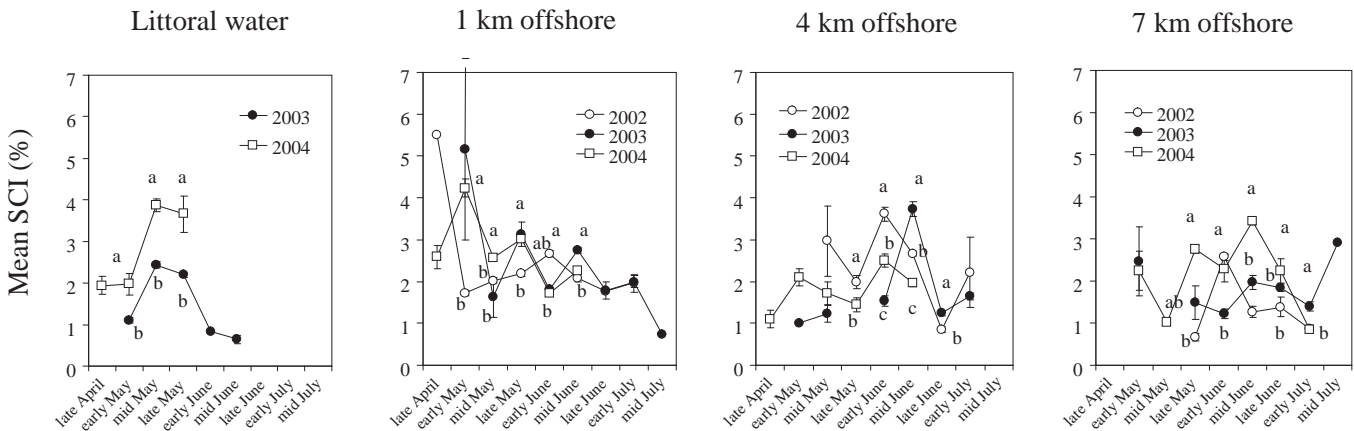

Fig. 9. Changes in mean values (with S.E.) of stomach content indices (SCI: stomach content weight x 100 / body weight) of juvenile pink salmon captured at the littoral site and the 1 km, 4 km and 7 km transects off the Abashiri coast in Okhotsk Sea from 2002 to 2004. The values not sharing a common small letter among years are significantly different at *p* < 0.05.

ous in offshore rather than nearshore waters.

Food Items

When comparing mean stomach contents indices (SCI) of pink salmon juveniles among the three years, different trends were found at different locations. While the fluctuating patterns in SCI in littoral waters in 2003 and 2004 were very similar, with a peak in early and mid May, SCI in 2003, when more fish were present, were significantly lower than those in 2004 (Fig. 9). At the 1 km transect, SCI in three years tended to be higher early in the season when pink salmon were more abundant than later in the season when the number of pink salmon decreased rapidly. In contrast, SCI at the 4 km transect tended to be lower early in the season when fewer fish were present than late in the season when more fish were present. In particular, SCI in 2003 was lower early in the season than in other years. However, when

fish dispersed in late June, SCI in 2002 and 2003 decreased markedly. At the 7 km transect there were significant differences in SCI in all three years. From late May to late June when more fish were present, SCI in 2004 were higher than those in 2002 and 2003 except for early June in 2002. In late June when most of pink salmon juveniles had dispersed, SCI at the 4 and 7 km transects decreased.

Diet analysis revealed that juvenile pink salmon at the 1 km and 4 km transects in 2002 consumed primarily cold-water species of copepods (mainly *Pseudocalaunus newmani*, *Neocalanus* spp.) and appendicularians (mainly *Fritillaria borealis* f. *typica*) in May, switching to warm-water species of cladocerans (mainly *Podon leuckarti*, *Evadne nordmanni*), appendicularians (mainly *Oikopleura longicauda*) in June (Fig. 10). In contrast, juvenile pink salmon at the 7 km transect consumed a varied diet including amphipods, insects and fish eggs. Jacobs' (1974) electivity indices showed pink salmon in 2002 favored cladocerans in May and June
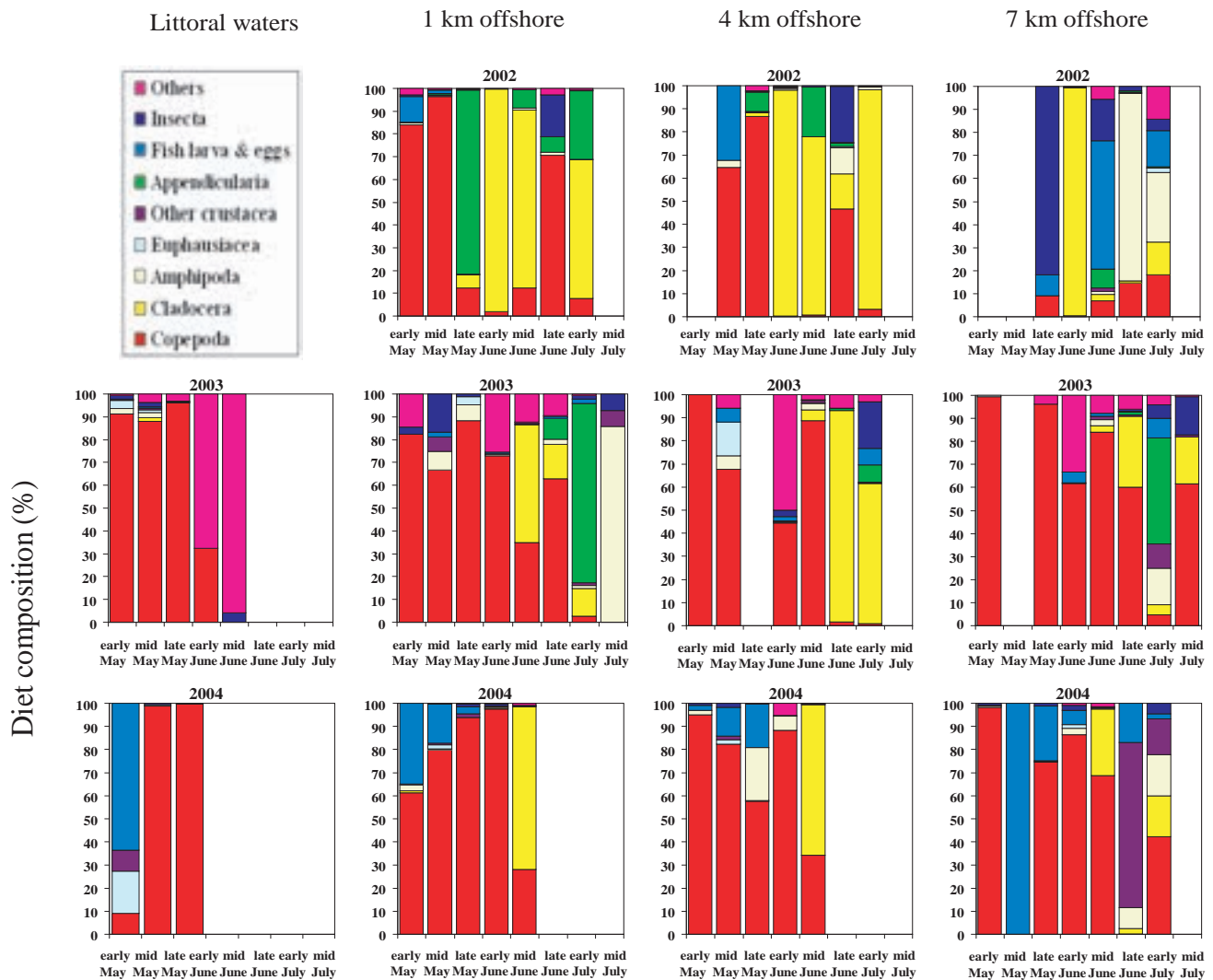
Fig. 10. Changes in diet composition (by number) of pink salmon juveniles at the littoral site and the 1 km, 4 km and 7 km transects off the Abashiri coast in Okhotsk Sea from 2002 to 2004.

when the water was warm, but preferred copepods early in the season (Fig. 11). While juveniles in coastal waters in 2003 consumed predominantly copepods (mainly *Pseudocalaunus newmani*, *Eurytemora herdmani*, *Acartia hudsonica* and *Metridia pacifica*) until mid June, differing from 2002, their diets later became dominated by cladocerans (mainly *Podon leuckarti*), and appendicularians the same as in 2002. Jacobs' electivity indices in coastal waters showed that pink salmon in 2003 favored copepods early, but switched to cladocerans and appendicularians later. Diet composition of pink salmon juveniles in the littoral zone in 2003 was different from that for fish in coastal waters. Juveniles in the littoral zone consumed not only pelagic copepods but also epibenthic crustaceans such as Harpacticoida copepods, indicating that juvenile pink salmon can change their feeding behavior depending on nursery conditions. Although in 2004, diet composition in coastal waters also included copepods early in the season, not only small coastal species

such as *Pseudocalanus newmani*, *Tortanus discaudatu*, *Eurytemora herdmani*, but also large oceanic copepods such as *Neocalanus* spp. were comsumed. By mid July, the contribution of copepods to their diet composition decreased as they switched to cladocerans (*Evadne nordmanni*), amphipods and fish eggs. Jacobs' indices also revealed that pink salmon in 2004 preferred copepods early, switching to cladocerans later in the season. Amphipods were favored throughout the season except for sometimes at the 7 km transect. Diet composition in littoral waters in 2004 was clearly different from that in 2003 and was dominated by pelagic copepods such as *Neocalanus* spp, *Sinocalanus tenellus*, *Pseudocalanus newmani*, *Eurytemora herdmani*.

DISCUSSION

Great differences in spatial distribution, abundance and size of juvenile pink salmon were found over three years in
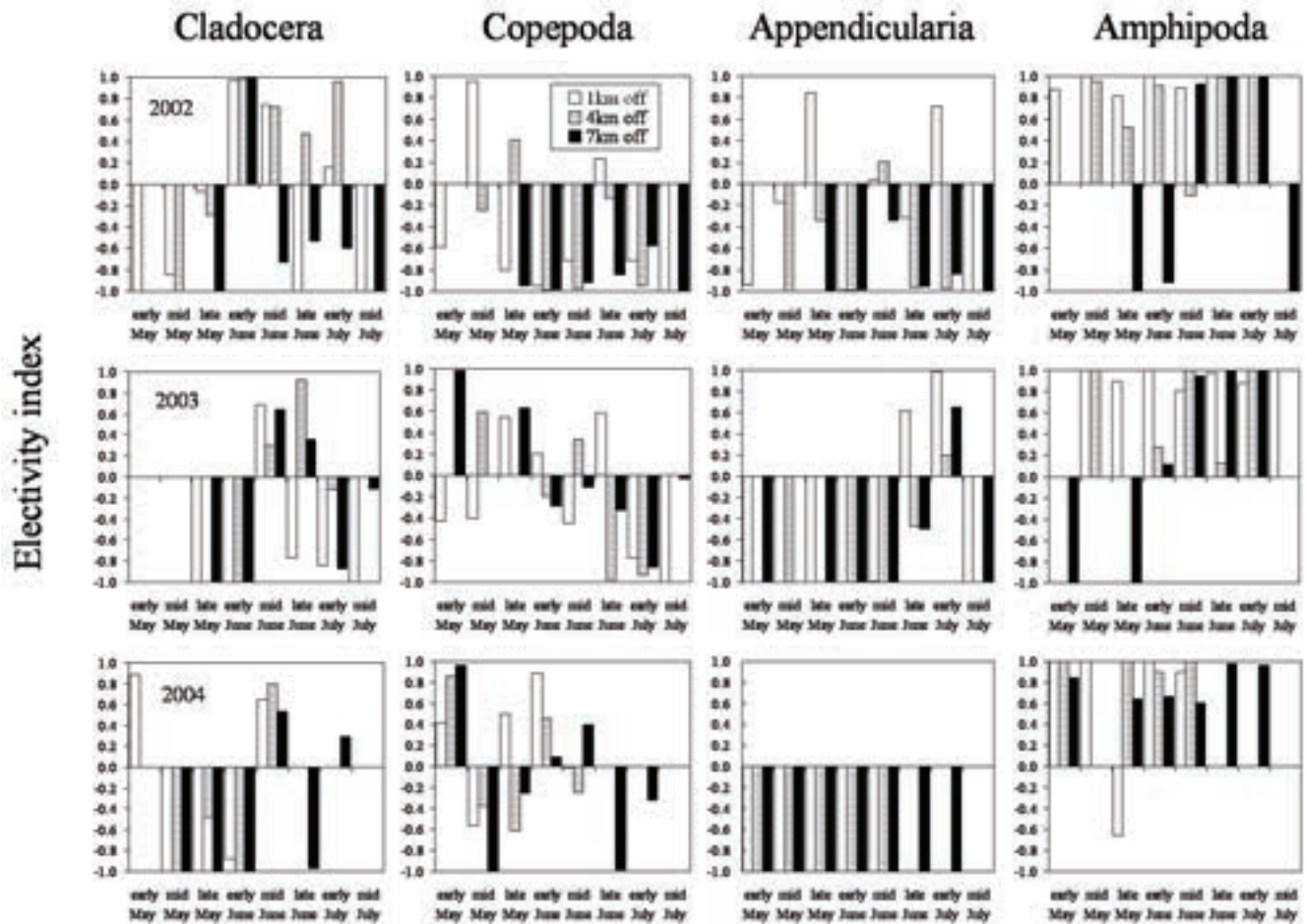
Fig. 11. Changes in electivity indices (by number) of four prey groups. Electivity (Jacobs 1974): E = (ri - Pi) / (ri + Pi - 2ri · Pi), ri: % of i species in stomach contents, Pi: % of i species in coastal waters. +1 = positive preference, -1 = negative preference.

Abashiri coastal waters. In the cool year, 2003, juvenile pink salmon in May were restricted to littoral waters as shown by the CPUE results, while juvenile pink salmon in the warm years, 2002 and 2004, were distributed widely along the 1 km offshore transect with only a short residence time in littoral waters. This pattern was strongly correlated with differences in SST between cool and warm years. Offshore movement of pink salmon is known to be size-dependent, with larger juveniles moving offshore earlier (LeBrasser and Parker 1964; Healey 1980). However, no clear differences in fish size early in the season were found, not only among years until mid May, but also among locations (1 km, 4 km and 7 km offshore transects) in 2003 and 2004, the exception being 2002. Therefore, we hypothesize that cold temperatures < 8°C in coastal waters may restrict the movement of pink salmon juveniles after seaward migration.

However, another hypothesis may also be proposed because the origin(s) of captured pink salmon were unknown. The timing of the downstream migration of pink salmon in 2003 might be different from that in 2002 and 2004 because of differences in spawning times and/or stream water temperatures. For example, while the pink salmon juveniles captured in the littoral waters in May 2003 were composed of early-migrating (or early spawning) fish, other juveniles in 2003 may have been delayed in migrating to sea in June. It is not known whether pink salmon captured in both littoral and coastal waters were of the same origin or cohort because no fish were marked. However, we stocked ALC-marked chum salmon juveniles from 2002 to 2004 during the pink salmon survey. Many marked chum juveniles were captured in littoral waters in May 2003 when no marked chum were caught at the 1 km offshore transect (Nagata et al. 2007). These observations strongly support the first hypothesis that seawater temperatures < 8°C restrict pink salmon movement into coastal waters.

Moreover, differences in areas that pink salmon use as nursery grounds likely affect fish abundance and growth. Pink salmon in the warm years 2002 and 2004 were significantly larger than those in the cool year 2003, in particular in 2002 when pink salmon were always the largest at the 4 km and 7 km transects. Further, 2002 pink salmon were significantly larger at offshore locations than in nearshore

areas. This is consistent with previous research showing that offshore movement of pink salmon in North America is size-dependent (LeBrasser and Parker 1964; Healey 1980). In contrast, pink salmon in the cool year, 2003, were always the smallest in coastal waters despite not being significantly different from fish in littoral waters in 2004. Although the zooplankton bloom in spring 2003 was slightly delayed compared with other years (Asami et al. 2007), feeding activity of juveniles in 2003 did not seem to be high, judging from the fact that SCI in the littoral zone and at the 4 km offshore transect were significantly lower in 2003 than in other years. Also, pink salmon juveniles in 2002 and 2004 consumed more large-sized pelagic zooplankton (*Neocalanus* spp.) than in 2003. Stomach evacuation of pink salmon that ranged from 32 to 57 mm in length required 6 and 16 h at temperatures of 12.8°C and 8.5°C, respectively (Bailey et al. 1975), suggesting that pink salmon juveniles consume less food at cooler temperatures. In addition, juvenile chum salmon that were captured in coastal waters (Nagata et al. 2007) were reported to grow rapidly at 10–12°C, and slowly at 5°C (Kaeriyama 1986). Moreover, because pink and chum salmon lived together in dense aggregations and consumed almost same diet in littoral waters in 2003 (Nagata et al. 2007), it is very likely that intra- or inter-specific competition between them became greater than in other warmer years. Therefore, slow growth in 2003 may be the result of depressed feeding activity combined with intensified competition due to low water temperatures and larger aggregations of fish in a limited area. In contrast, rapid growth rates in the warm years, 2002 and 2004, may be related to more active feeding at optimal water temperatures and expanded feeding areas. The abundance of fish captured in coastal waters in the warm years, 2002 and 2004, was much higher than that in 2003 despite the fact that pink salmon in 2003 were more abundant in littoral waters.

Poor survival of pink salmon in 1991 and 1992 was reported in Prince William Sound, Alaska (Willette 1996; Willette et al. 2001). The authors recognized that slow-growing juvenile salmon living at very low ocean temperatures in the spring could have sustained high mortality in 1991 because they are vulnerable to size-selective predators for longer periods of time (Parker 1971; Healey 1982; West and Larkin 1987). Shimizu (2002) reported that the return rate for pink salmon from the 1967 to the 1995 brood years in the Okhotsk coastal region was negatively correlated with the concentration of sea ice, especially because the dramatic increase in the abundance of pink salmon since the 1990 brood year was coincident with a period characterized by much less sea ice. Sea water temperatures in the Abashiri coastal waters in spring are known to be affected by a combination of three influences: the Soya Warm Current with 33.6 psu and high temperatures; the Okhotsk surface water with 32.5 psu and temperatures 2-5°C (related to the distribution and movement of sea ice); and, the coastal waters that are influenced by freshwater inputs (Irie et al. 1981; Takizawa 1982).

Moreover, as the Okhotsk Sea is usually covered with sea ice during the winter, the timing of the appearance and disappearance of sea ice also affects oceanic parameters such as seawater temperature and the timing of plankton blooms in the spring (Shimizu 2005). In 2002 and 2004, the sea ice disappeared in early March, one month earlier than in 2003 that had the latest sea ice disappearance in the past 10 years (Shimizu 2005; Asami et al. 2007). Further, in 2003, movement of the front of the Soya Warm Current to the Abashiri coast was also delayed (Asami et al. 2007). As a result of these oceanographic conditions, the cold Okhotsk Surface Water occupied the coastal waters in May 2003 with SST ranging from 5.3–6.8°C, much colder than in the warm years (8.2–9.7°C in 2002, 5.5–12.0°C in 2004). Therefore, we conclude that temperatures in coastal waters strongly affect the residence time and the offshore movement of pink salmon juveniles after seaward migration and may be controlled by a combination of the amount and timing of sea ice formation and the Soya Warm Current (Asami et al. 2007).

The level of 2004 recruitment (adults) from the 2002 brood-year pink salmon that were juveniles in coastal waters in spring 2003 was much lower than the 2003 recruitment from the 2001 brood year which entered the sea in spring 2002. This reversal of the trend in adult returns between the two years resulted in the shift in dominance. As shown in Fig. 4, the SR index in 2001 brood-year pink salmon was the highest of the past odd-year brood stocks, suggesting that the survival rate in the 2001 brood year was high. Although relatively high mortality is known to occur in both the freshwater and ocean phases of the life cycle, pink salmon mortality during the ocean phase was more variable and higher than that during the freshwater phase (Manzer and Shepard 1962; Parker 1965, 1968; Healey 1991; Willette et al. 2001). In addition, the most probable cause of initial disparity between the two lines is either a disastrous decrease (or a dramatic increase) in the survival rate of one line over the other (Neave 1953; Ricker 1962). If our proposed scenario is true concerning the shift in pink salmon abundance in the Okhotsk Sea of Hokkaido, the shift in dominance lines might be caused by the thermal conditions that result in longer estuary residence times with larger aggregations of fish, or rapid dispersal with wider occupation of nursery grounds after seaward migration.

Unfortunately, we did not separate hatchery-reared pink salmon from wild pink salmon. Morita et al. (2006) estimated that the contribution of hatchery fish to pink salmon catches was 35.4% on average between 1971 and 2003. In 2005 ALC-marked pink salmon were stocked. This mass stocking of marked pink salmon will be continued for three years. Therefore, in the near future we will be able to determine the degree to which hatchery pink salmon contribute to the pink salmon population in the Okhotsk Sea coastal region.

ACKNOWLEDGEMENT

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Spatial and Temporal Changes in the Growth Patterns and Survival of Hokkaido Chum Salmon Populations in 1970–2001

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Abstract: The survival strategies of Pacific salmon (*Oncorhynchus* spp.) offer a useful framework for quantifying both inter- and intra-specific interactions and also climate-related risk factors around the North Pacific Rim. The annual growth patterns of adult chum salmon (*O. keta*) returning to the Ishikari River were estimated with the back-calculation method based on scale analysis. Their growth increased during the first year in the Okhotsk Sea in the 1990s. The growth in the first year was negatively correlated with the sea ice concentration in winter, and positively correlated with the sea surface temperature (SST) during summer and fall in the Okhotsk Sea, despite the lack of a relation between SST and zooplankton biomass. The positive correlation between the growth in the Okhotsk Sea and survival was also observed in Hokkaido chum salmon. In the Bering Sea, the relationship between residual carrying capacity and growth patterns of Hokkaido chum salmon indicated that the growth reduction is affected by changes in population density-dependence. Results of stepwise multiple regression analysis of the survival rate of Hokkaido chum salmon population on body size at release from the hatchery and growth in the Okhotsk Sea showed that chum salmon have periods of critical mortality in the early marine period and the first winter at sea.

Keywords: Hokkaido chum salmon, growth pattern, survival, Okhotsk Sea, Bering Sea

INTRODUCTION

For the last several decades, the Pacific salmon (*Oncorhynchus* spp.) has remained healthy because of large-scale hatchery programs and favorable oceanic conditions associated with long-term climate change and the climatic regime shift (e.g. Beamish and Bouillon 1993; Kaeriyama 1998; Klyashtorin 1998). Pacific salmon are an important keystone species, not only as a human food resource, but also as an important component of the ecosystem of the sub-arctic Pacific Ocean. They occupy more than four trophic levels in the sub-arctic food web (Aydin et al. 2003; Kaeriyama 2003). Thus, the life history of salmon offers a useful framework for quantifying inter- and intra-specific interactions and climate-related risk factors around the North Pacific Rim.

Two hypotheses attempt to define the period of critical mortality in Pacific salmon: (1) size-selective mortality occurs during the early marine period (Healey 1982), and (2) salmon mortalities during the first marine fall and winter result from insufficient summer growth (Beamish et al. 2004; Moss et al. 2005). Hokkaido chum salmon (*O. keta*) are widely distributed throughout the North Pacific Ocean,

the Okhotsk Sea, and the Bering Sea. After spending their early marine lives in the coastal waters of Hokkaido in the spring, they spend their first summer and fall in the southern part of the Okhotsk Sea (< 50°N); they then move to the Western Subarctic Gyre for their first winter (Urawa et al. 2001). Thereafter, these chum salmon migrate between their summer feeding grounds in the Bering Sea and their over-wintering grounds in the Alaskan Gyre (Urawa 2000; Urawa et al. 2005). After about four years, they return to their natal rivers to spawn.

In this paper, we analyzed the spatial and temporal growth and survival patterns of Hokkaido chum salmon in the Okhotsk and Bering seas, and related climate change to their life-history strategies.

MATERIALS AND METHODS

In 1970–2001 (except for 1973 and 1985), the scales of age-4 (four-year-old) adult female chum salmon returning to the Ishikari River were collected and measured with a scale image processor (Ratock System Engineering Co.) to provide an index of growth. Each year for approximately 30

scales we calculated length along the long axis (measured to the nearest μ), the number of circuli from the focus to the inner edges of the check (R_{cj} and R_{os}), and individual annuli (r_1–r_4). The R_{cj}, R_{os}, and r_1–r_4 variables indicate scale radii from one to four years, respectively, in coastal Japan and the Okhotsk Sea (Fig. 1). Individual growth in fork length was calculated from the following formulae based on Kaeriyama (1998):

$$S_t = \sum_{i=1}^{t} r_i$$
$$FL_t = 0.0358(S_t - 114)^{1.2406} + 40$$
$$L_t = FL_t - FL_{t-1}$$
$$L_{cj} = 0.0358(R_{cj} - 114)^{1.2406} + 40$$
$$L_{os} = L_1 - L_{cj}$$

where r_i, S_t, FL_t, L_t, L_{cj}, and L_{os} are scale radius at age i, scale length from focus to the inner edges of age t annuli, fork length at age t, and growth at age t, for salmon from coastal Japan and the Okhotsk Sea. The values '114' and '40' express focus radius and fork length at the first scale formation.

The Meteorological Agency of Japan provided us with mean monthly sea surface temperatures (SST) per 1° latitude and longitude blocks (25–49°N, 121–180°E) for 1950–2004. We also used the satellite data of the AVHRR/NOAA (50–56°N, 145–155°E) for the SST for 1985–2004, and the SeaWiFS data on chlorophyll-*a* for 1998–2004 (50–56°N, 145–155°E).

Parameters of Ricker's recruitment curve ($R = \alpha Pe^{-\beta P}$) were estimated for year-classes of Hokkaido chum salmon (20 brood years) by the Levenberg-Marquardt method. From the recruitment curve, the replacement level (ln $(\alpha)/\beta$) was defined as the index of carrying capacity (Kaeriyama 2003). The residual carrying capacity (RCC) was defined as:

$$\text{RCC (\%)} = (\text{CC - R}) / \text{CC} \times 100$$

where CC and R are the carrying capacity and mean popu-

lation size (the return), respectively, for 20 brood years at Hokkaido. The relationship between the RCC and mean fork length of age-4 adult females or mean age at maturity for each year-class returning to 11 rivers in Hokkaido (Kaeriyama, 1998) were estimated by simple regression analysis. Relationships among return rates of Hokkaido chum salmon populations, body weights of juveniles released, and growth in the first year were evaluated by stepwise multiple regression analysis.

RESULTS AND DISCUSSION

Annual Change in the Growth Patterns of the Ishikari River Chum Salmon Population

The results of our study on annual changes in the growth patterns of Ishikari River chum salmon are shown in Fig. 2. In all age groups, growth during the first year increased in the 1990s. This growth increase occurred in the Okhotsk Sea, but not in the coastal waters of Hokkaido. However, growth in subsequent years decreased from the 1980s to the mid-1990s. In particular, the reduction in growth was considerably greater during the third year than in any other year in the Bering Sea.

Growth Pattern in the Bering Sea

Significant positive correlation was observed between annual growth and fork lengths of Ishikari River female chum salmon from the second to fourth years ($r > 0.48$, $P < 0.01$) despite the lack of a correlation in the first year ($r = -0.21$, $P = 0.40$; Table 1). We evaluated the relationship between the fork length of Ishikari River chum salmon and the RCC of Hokkaido chum salmon populations. Fork length declined with a decrease in the RCC (Fig. 3). At < 10% of the RCC, the fork lengths of age-4 female chum salmon reached their biological minimum size (64 cm) in the Ishikari River. The RCC was significantly positively correlated with body size and negatively related to age at maturity in Hokkaido chum salmon (Yatsu and Kaeriyama 2005). This phenomenon indicates a density-dependent effect (e.g. chum salmon: Kaeriyama 1989; Ishida et al. 1992; Helle and Hoffman 1998, sockeye salmon: Rogers 1980; Rogers and Ruggerone 1993). Thus, these results suggest that the growth of Hokkaido chum salmon will be affected by the interaction between the
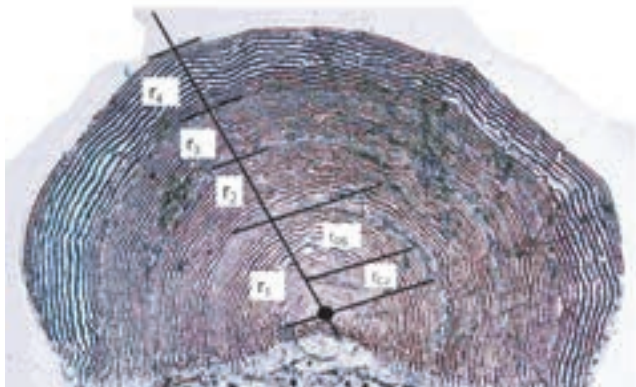

Fig. 1. Measurements of chum salmon scales. r_1-r_4: scale radius of individual annuli; r_{cj}: scale radius in the coastal waters of Hokkaido; r_{os}: scale radius in the Okhotsk Sea.

Table 1. Relationships between annual growth and fork length at maturity of age-4 female chum salmon returning to the Ishikari River during 1970–2001.

Age	Slope	Constant	r	F	P-value
First	-0.21	730	-0.16	0.74	0.40
Second	1.06	520	0.49	9.05	0.005
Third	1.14	538	0.76	38.28	<0.001
Fourth	1.04	561	0.63	18.10	<0.001
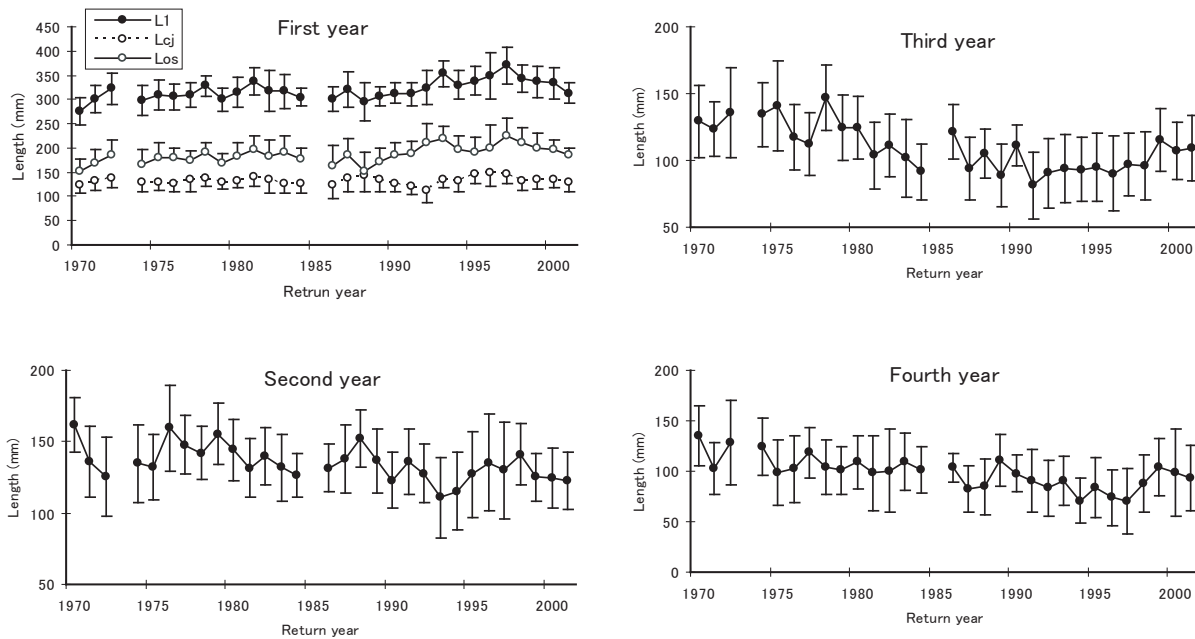
plankton biomass (r = -0.12, n = 44, F = 0.62, P = 0.43; Fig. 6B).

It is generally believed that the timing and duration of sea ice cover and winter wind currents determine the onset of spring primary production. Hunt et al. (2002) proposed the oscillating control hypothesis, which predicts that pelagic ecosystem function in the southeastern Bering Sea will alternate between primarily bottom-up control in cold regimes and primarily top-down control in warm regimes. Late ice
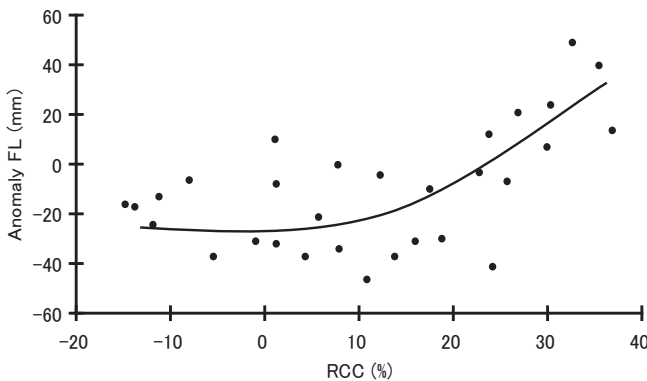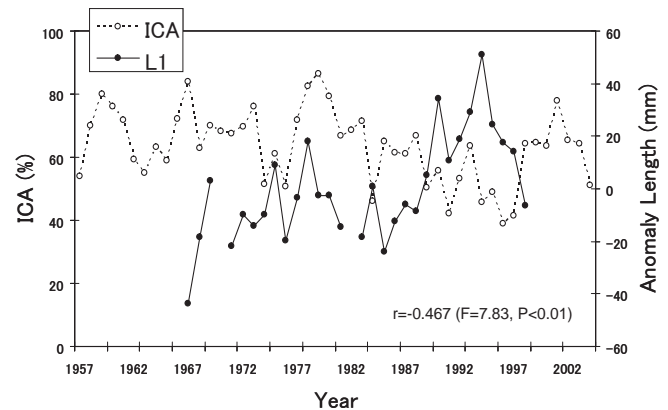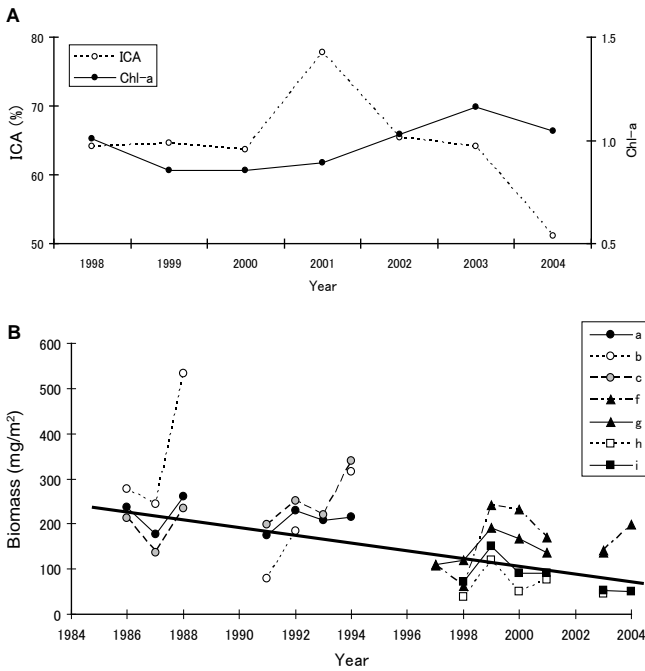
Fig. 6. Annual changes in the ice cover area (ICA), chlorophyll-*a* (A) and zooplankton biomass (B) in the Okhotsk Sea. a) Southern Okhotsk Sea; b) West Kamchatka area: north of 54ºN; c) West Kamchatka area: south of 54ºN (Shuntov and Dulepova 1996); f) Northern Okhotsk Sea: spring; g) Northern Okhotsk Sea: fall; h) Southern Okhotsk Sea: summer; i) Southern Okhotsk Sea: fall (Merzlyakov et al. 2005).
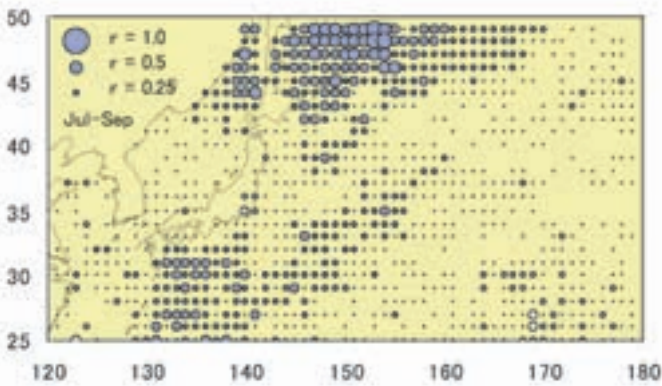
Fig. 7. Correlation between SSTs during summer and fall, and growth anomalies in Ishikari River chum salmon in the Okhotsk Sea for 1967–1998. Solid and open circles indicate positive and negative correlation coefficients, respectively.

retreat (late March or later) leads to an early, ice-associated bloom in cold waters, whereas no retreat or early ice retreat (before mid-March) leads to an open-water bloom in warm waters in May or June. Regulated by productivity and predation, zooplankton populations are not closely coupled to the spring bloom, but are sensitive to water temperature. Zooplankton population size is limited by bottom-up food shortages and top-down predators. Both limitations are central to the control of energy flow in the southeastern Bering Sea ecosystem. In the Okhotsk Sea, however, neither chlorophyll-*a* nor zooplankton populations were closely coupled to the ICA in winter and SST in summer and fall. Therefore, it is difficult to adopt the oscillating control hypothesis (Hunt et al. 2002) for the mechanism(s) of primary production in the Okhotsk Sea.

The correlation map indicated a strong positive correlation between growth anomalies in Ishikari River chum salmon and SSTs during summer and fall in the Okhotsk Sea (Fig. 7). This result suggests that growth in Ishikari River chum salmon will be affected by SSTs during summer and fall and not by productivity trends such as chlorophyll-*a* and zooplankton biomasses.

Growth and Survival in the First Year at Sea

Figure 8 shows changes in the growth of Ishikari River
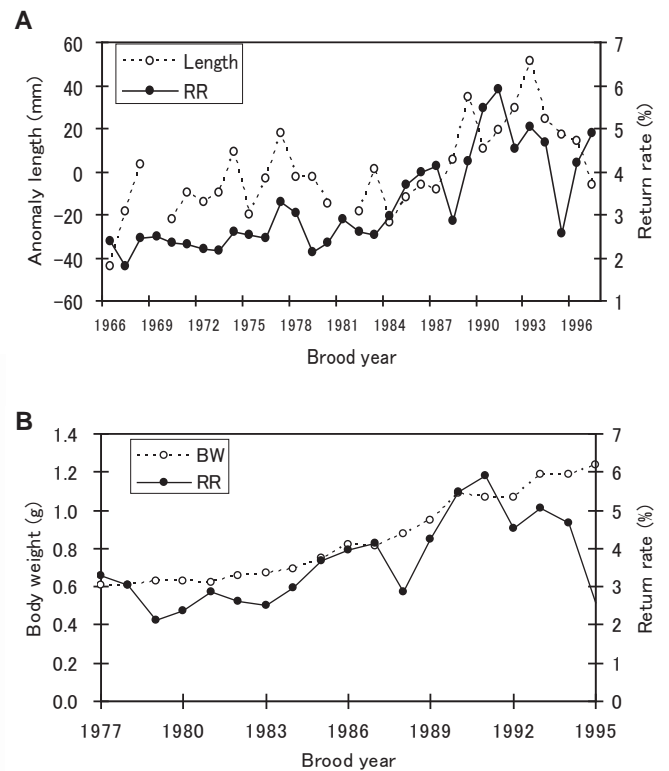
Fig. 8. Changes in growth anomalies (length, A) after Ishikari River chum salmon's first year, mean body weights (BW, B) of released juveniles, and return rates (RR) of Hokkaido chum salmon populations.

Table 2. Result of the stepwise multiple regression analysis of the return rates of Hokkaido chum salmon populations, mean body weights of released juveniles, and the mean growth rates of Ishikari River chum salmon during their first year.

Variable	Slope	Partial correlation	*T*	*P*
Mean body weight of juvenile released	4.003	0.700	3.797	0.002
Growth at the first year	0.002	0.039	0.152	0.881
Constant	0.876		0.240	

$r^2 = 0.685$, df: $n1 = 2$, $n2 = 15$, $F = 16.32$, $P < 0.001$, AIC = 41.404

chum salmon in their first year, the mean body weight of released juveniles, and the return rate of Hokkaido chum salmon populations. The return rate is defined as the survival rate from release to return. The return rate correlates not only with the growth of salmon in their first year ($r = 0.672$, $n = 30$, $F = 23.04$, $P < 0.001$), but also with the body size of juveniles released ($r = 0.763$, $n = 19$, $F = 23.65$, $P < 0.001$). However, the result of a stepwise multiple regression analysis on the return rate of Hokkaido chum salmon populations revealed that (1) the body size of juveniles at their release, and (2) growth in the Okhotsk Sea did not correlate well with survival rates (Table 2).

Two hypotheses address the period of critical mortality in Pacific salmon: (1) Size-selective mortality occurs in the early marine period (Healey 1982); and (2) Size-related mortality during the first marine fall and winter results from insufficient growth by the end of the first marine summer (Beamish et al. 2004). Pink salmon released from the hatchery at Prince William Sound in Alaska illustrated that marine survival after the first growing season is related to increases in early marine growth, and that larger and faster-growing juveniles have a higher survival rate (Moss et al. 2005). The return rate and carrying capacity of Hokkaido chum salmon populations did not relate to indices of long-term climate change, such as the Atmospheric Circulation Index and the Aleutian Low Pressure Index (Kaeriyama 1999; Yatsu and Kaeriyama 2005). Our results suggest that Hokkaido chum salmon will be affected by size-related mortality in the first marine winter after their rearing period in the Okhotsk Sea. However, mortality rates in the early marine period will be higher than those during their first marine winter.

CONCLUSION

In the Okhotsk Sea, the temporal increase in SST will result in the growth and survival of Hokkaido chum salmon populations, although this change will not affect trends in productivity. The survival strategies of Pacific salmon offer a useful framework for evaluating not only inter- and intra-specific interactions but also climate-related risk factors throughout the North Pacific. The growth patterns of Hokkaido chum salmon will be controlled by ocean conditions such as SST and ice cover in the Okhotsk Sea, and by inter- and intra-specific interactions such as carrying capacity and population density in the Bering Sea.

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Bioenergetic Responses by Pacific Salmon to Climate and Ecosystem Variation

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Abstract: Salmon growth can respond to changes in temperature, food availability, food quality, and activity. Climatic variability can affect one or more of these factors, because different climate regimes are associated with different temporal-spatial patterns of temperature, salinity, and other oceanographic features that can alter ocean distribution patterns of salmon and cause shifts in assemblages of other organisms. Consequently, climate variability can simultaneously change the availability or productivity of exploitable prey, and the intensity of competition or predation experienced by salmon at various stages of ocean life. Variability across multiple factors can potentially confound the understanding and prediction of salmon growth or survival. Bioenergetics models can account for changing thermal and food conditions explicitly, and are valuable analytical tools for isolating and evaluating the relative contribution of different factors (e.g., temperature, feeding rate, food availability, food quality) to the consumption and growth of salmon during different life stages. Model simulations, coupled with data on growth trajectories, diet composition, and thermal experience, provide estimates of: 1) consumption rates on each prey (measures of both the importance of various prey to the energy budget of salmon, and the predation impact of salmon on prey species); 2) feeding rate as a proportion of the theoretical maximum consumption rate, a measure of relative food availability; and 3) growth efficiency, a measure of how much food was required to achieve the observed growth rate. We applied bioenergetics models to juvenile pink salmon in the Gulf of Alaska during years of low (2001) versus high (2002) ocean survival to examine feeding and growth performance between years while explicitly accounting for significant variability in stage-specific distribution, diet, growth, and consumption. From these simulations, we determined that higher feeding rates on pteropods, primarily during July–August 2002, explained the higher growth rates and larger body mass of juveniles that were associated with higher stage-specific marine survival for juveniles in 2002. Current bioenergetics models for salmonids provide valuable diagnostic and analytical tools. However, as modeling applications become more predictive and demanding, modifications and improvements will be required to address important topics like behavior, variable activity costs, seasonal and ontogenetic energy allocation, and foraging models.

Keywords: salmon, feeding rate, temperature, climate, food supply, bioenergetics, marine survival, ecosystems

INTRODUCTION

Climate change can impose direct and indirect effects on the energetics of Pacific salmon in marine ecosystems, and these effects can have both immediate and delayed consequences for their growth and survival. Climate-driven changes in the physical characteristics of water masses determine temporal-spatial patterns of temperature, salinity, light, and nutrients in the epipelagic waters inhabited by salmon (Hare and Francis 1995; Mantua et al. 1997; Batchelder and Powell 2002). Direct behavioral responses can alter movement and distribution patterns of salmon in coastal, shelf, and open ocean environments. Direct metabolic responses to different temperatures or salinities determine what fraction of an organism's energy budget must support basal and active metabolism rather than be allocated into somatic growth, reproduction, or high-energy lipid storage.

Climate change can also affect the energetics of salmon indirectly by altering other biological components of the ecosystem. Biotic responses to the physical environment

are expressed as differences in the species composition and productivity of phytoplankton, zooplankton, and vertebrates associated with different water masses (Brodeur et al. 2004; Coyle and Pinchuk 2005), and are modified by the trophic dynamics among these organisms (Aydin et al. 2005). The interacting effects of food supply, competition, predation, environmental stressors, and disease determine the growth and survival of Pacific salmon. Trophic dynamics and these other processes are mediated to some degree by ambient environmental conditions which vary through time and space, and consequences for growth or survival can differ among sizes or life stages.

Climate change can affect all life stages of salmon through temporal-spatial changes in the physical environment and biological responses, leading to immediate or delayed consequences for survival or growth. The energy stores of returning adults determine their ability to reach the spawning grounds, find, prepare, and defend stable redd sites, select quality mates, and produce high numbers of embryos with the highest possible probability of survival. For smolts, factors affecting spawning, incubation, or freshwater rearing conditions could alter their vulnerability to predation or create spatial-temporal mismatches in foraging conditions during early marine life.

Climate-forcing can affect the distribution (Welch et al. 1998), feeding, growth, and survival for juvenile and older life stages of salmon in freshwater, estuarine, and marine habitats (Furnell and Brett 1986; Fisher and Pearcy 1988; Hinch et al. 1995). Many species of salmon exhibit coherent growth and survival patterns at regional spatial scales (i.e. 100–500 km), thus suggesting that overall ocean performance is influenced by environmental or ecological conditions experienced in localized regions during early marine life, but that conditions and performance differ among regions (Mueter et al. 2002, 2005; Pyper et al. 2005).

Distribution and movement patterns will influence temporal-spatial overlap of salmon with food (Aydin et al. 2005), potential competitors and predators, whereas ambient temperature determines the amount of prey that can be consumed, and temperature, activity rates, and prey quality will determine the efficiency with which ingested energy can be converted into growth. The energetic status of adults in the ocean influences the allocation of energy to gonadal and lipid stores, whereas ocean distribution patterns will determine the time and energy required for migration back to the spawning grounds (Blackbourne 1987; Welch et al. 1998). Time and energy shifts away from foraging to migration mean less energy acquired from foraging but more energy spent migrating (Nottestad et al. 1999). Because adult salmon often acquire significant fractions of their maximum body mass and energy during the final months of ocean growth, the timing, location, and degree of transition from feeding to migration activity likely involves significant evolutionary trade-offs between the benefits and consequences of arrival timing on the spawning grounds and the energetic scope for reproductive investment and activity.

Size-selective mortality has commonly been invoked as an important factor influencing survival of juvenile salmon in freshwater, estuarine, and marine habitats (Parker 1968; Hartt 1980; Healey 1982; Bax 1983; Holtby et al. 1990; Koenings et al. 1993; Willette et al. 1999; Beamish and Mahnken 2001; Moss et al. 2005). Growth integrates the combined effects of feeding rate, food quality, temperature, and additional metabolic costs attributed to unusual levels of activity or environmental stress. Therefore, these factors that affect juvenile growth performance and body size should be linked to survival at current or subsequent life stages.

The quantity and quality of exploitable prey can vary spatially and temporally in response to climate-driven bottom-up control (Fisher and Pearcy 1988; Aydin et al. 2005; Coyle and Pinchuk 2005; Zamon and Welch 2005), but if food supply is limiting, intra- or inter-specific competition could exacerbate localized reductions in food (Ruggerone et al. 2003; Beauchamp et al. 2004; Ruggerone and Goetz 2004). Organisms are termed "exploitable prey" here if they commonly contribute significant fractions of the biomass in the diet (e.g., prey contribution ≥ 10% of the average diet contents by wet weight), if they fall within the edible size ranges consumed by salmon, and if these prey are available at locations, depths, and times that salmon can detect and feed on them. Juvenile salmon in marine systems generally feed during daylight (Armstrong et al. 2005) in the upper mixed layer (e.g., 0–10 m or 0–20 m depths) on prey ≥ 1 mm; therefore, estimates of prey availability should be filtered through similar temporal, spatial, and size-based criteria. Prey quality can affect net energy intake rate. Prey quality explicitly includes energy density ($J \cdot g^{-1}$ wet body mass), body mass (g wet body mass), and digestibility (indigestible proportion of the body mass) of prey, whereas differences in prey detection, capture, and handling times are generally only implicitly reflected in measures of diet composition and prey electivity.

Understanding the effects of climate change is complicated because of the simultaneous change across a suite of physical and biological factors that directly or indirectly influence growth and survival of salmon in the ocean; however, bioenergetics modeling provides a conceptual framework to mechanistically account for energetic responses to changing temperature, diet, body size and growth (Brandt and Hartman 1993; Ney 1993). Bioenergetics models are energy balance equations where energy inputs from consumption equal energy losses due to metabolism and waste, with the remaining energy surplus or deficit allocated to growth (or weight loss) of the consumer. The Wisconsin Bioenergetics Model (Hanson et al. 1997) is the most widely used form of this type of model (Hansen et al. 1993; Ney 1993) and provides parameters for numerous freshwater and some marine species of fish and several invertebrates.

The models for Pacific salmon (Beauchamp et al. 1989; Stewart and Ibarra 1991) and steelhead (Rand et al. 1993)

contain weight-dependent functions for maximum daily consumption and metabolism, temperature-dependent functions for maximum daily consumption and metabolism (basal respiration and activity), and a temperature- and ration-dependent function for waste. Specific dynamic action (SDA) is treated as a constant proportion of consumption. The model operates on a daily time step, thus enabling simulations to account for changing conditions at fine-scale temporal resolution, if appropriate.

For many species, including Pacific salmon, parameters have often been "borrowed" from other species, thus calling into question how accurately the specific physiological responses of a species can be simulated (Boisclair and Tang 1993; Ney 1993; Trudel and Welch 2005). Despite these concerns, salmonid models have generally performed well at estimating consumption when compared to independent measures of consumption and growth in controlled laboratory conditions (Madenjian et al. 2004), or to estimates of *in situ* consumption in both freshwater (Beauchamp et al. 1989; Ruggerone and Rogers 1992) and marine environments (Brodeur et al. 1992). In these cases, the model produced consumption estimates within ± 10% of independently derived, field-generated estimates for the same consumers, and these examples were applied to the same life stages or size ranges as that of salmon spending their first growing season in the ocean. Although comparing one estimate to another does not ensure that either one represents the true value, such corroborations encourage confidence in these approaches and support the applications of these models to compare consumption and growth performance, in at least relative terms at a minimum, with reasonable expectation that the model estimates are considerably better than that. When evaluating these models, the key consideration should be the level of uncertainty associated with a specific application of the model (i.e., estimation of consumption versus estimating growth, respiration, or waste).

Because growth is easier to estimate than consumption, and is more commonly measured in field studies, the most common application of these models has been to compute the consumption (in terms of biomass and associated energy of prey) required to satisfy a particular growth rate, given the body mass, thermal experience, and diet of the consumer. Conversely, the model can compute growth, given a specified level of energy consumption and thermal experience. In this latter application, independent estimates of consumption are rare, so this approach often relies on foraging models that use either a functional response model (Stockwell and Johnson 1997, 1999) or a prey encounter-capture rate model (Burke and Rice 2002; Mazur and Beauchamp 2006).

The objectives of this paper are: 1) to describe how bioenergetics modeling, when coupled to directed field sampling, can quantify consumption rates or growth performance of salmon in the wild by accounting for effects of feeding rate (an indicator of food supply), prey quality, temperature, and body size; 2) to provide an example application of this

approach that contrasts juvenile pink salmon growth in the coastal Gulf of Alaska (GOA) during years of low versus high marine survival; and 3) discuss some important limitations and suggested improvements for the model with respect to current and future applications.

METHODS

Simulating Consumption and Growth Performance with a Bioenergetics Model

We used the physiological functions for pink/sockeye salmon in the Wisconsin bioenergetics model (Hanson et al. 1997) to demonstrate how salmon would be expected to respond to changes in body size, temperature, feeding rate, and food quality over a range of conditions that were relevant to the first year of ocean growth. Parameters from the sockeye salmon model (Beauchamp et al. 1989) have been used as a surrogate pink salmon model (Hanson et al. 1997; Aydin et al. 2005; Cross et al. 2005). All of the salmonid bioenergetics models (with the exception of lake trout), share the same functional forms of equations for maximum consumption, metabolism and waste, although the parameter values differ somewhat among species (Hanson et al. 1997). Therefore, the description using the sockeye/pink salmon model should apply to general relationships for other salmonid species, although the actual magnitude of the responses at different body sizes or temperatures differ among species due to species-specific parameterizations of these functions.

We generated response curves from the model to compare the relationship between maximum consumption C_{max} and metabolism (standard + active respiration costs) over a range of body masses (0.3–300 g) to demonstrate how allometric responses lead to differences in the ratio of gross food intake to metabolic costs through the ontogeny of fish. To compare C_{max} and daily metabolic rates (standard, active, and SDA) in comparable units, metabolic rates were converted from energy rates ($J \cdot g^{-1} \cdot d^{-1}$) into mass equivalents of food ($g \cdot g^{-1} \cdot d^{-1}$), assuming a prey energy density of 4000 J/g. Modeled values for C_{max}, C_{max} – waste, and metabolism were plotted across a range of temperatures (0–25°C) for a 10-g sockeye/pink salmon. The resulting temperature-dependent growth rates were computed for a 10-g fish eating at C_{max}:

$$\text{Growth} = C_{max} - \text{Waste} - \text{Metabolism}$$

These calculations were repeated for a 100-g consumer to demonstrate the proportional difference in scope for growth as a proportion of consumer body mass ($g \cdot g^{-1} \cdot d^{-1}$).

To examine the predicted temperature-dependent growth response of juvenile salmon to different daily ration sizes and prey quality, the daily growth rate for a 10-g salmon was simulated at 1°C temperature increments for one day over a range of 0–25°C. The simulations were run at daily consumption rates of 100%, 50%, and 20% of C_{max} (*p*-value =

1.0, 0.5, and 0.2 in the Wisconsin model, respectively). The prey energy density for these simulations was set at 2800 J/g to emulate a relatively low-energy diet composed primarily of copepods and pteropods (Davis et al. 1998; Aydin et al. 2005). To demonstrate the effect of higher prey quality on growth, the low-feeding rate simulation (20% C_{max}) was repeated using a higher prey energy density of 5000 J/g to emulate a diet composed primarily of higher quality prey like euphausiids, larval/juvenile fish, and squid (Aydin et al. 2005).

Simulations of Pink Salmon in the Coastal Gulf of Alaska

The bioenergetics model was used to evaluate growth performance and consumption requirements of juvenile pink salmon during their first growing season in Prince William Sound (PWS) and the coastal Gulf of Alaska (CGOA) during contrasting years of low marine survival (2001, average hatchery juvenile-adult survival S = 3%) and three-fold higher survival (2002, S = 9%). Spatial-temporal distribution, diet, thermal experience, and juvenile growth rates also differed considerably between 2001 and 2002, in addition to the difference in survival.

We focused on identifiable release groups from PWS hatcheries both because marine survival rates could be linked directly to these groups, and to minimize variation due to size, location, and timing of entry and prior growth history from the broader mix of stocks co-occurring in these samples. PWS hatcheries applied unique thermal otolith marks to each release group; thus the origin, time, and average size at release could be linked to hatchery fish subsequently captured at various life stages by decoding their otolith marks. The modal juvenile feeding and growth conditions for these hatchery groups were simulated by entering the weighted-average size, growth, diet, and temperature regimes (Armstrong et al. 2005; J. Armstrong and A. Cross, unpublished data) from the water masses yielding the highest catch per unit effort (CPUE) of hatchery salmon each month as inputs to the bioenergetics model (Table 1). Monthly energy densities measured for pink salmon in Prince William Sound were taken from Boldt and Haldorson (2002), and prey energy densities were taken from literature values (Davis et al. 1998; Cross et al. 2005) and direct laboratory measurements (Mazur et al. 2007) of the major prey organisms (Table 2).

Juvenile pink salmon were sampled monthly from July through September or October 2001 and 2002 at three locations in PWS (PWS 1–3) and six stations along the GLOBEC-designated Seward line (GAK 1–6). Fork lengths (FL, mm) at specific life stages were back-calculated from scale circuli spacing patterns (Courtney et al. 2000; Fisher and Pearcy 2005; Moss et al. 2005) based on regressions of FL versus the radius of the total scale size (SS, μm) for PWS hatchery fish sampled in PWS and CGOA during 2001 (see Moss et al. 2005; $R^2 = 0.78$, $p < 0.001$):

$$FL = 0.216 \cdot SS + 44.49$$

and during 2002 ($R^2 = 0.77$, $p < 0.001$):

$$FL = 0.202 \cdot SS + 47.42$$

The back-calculated stage-specific lengths were converted to body mass (W, g wet weight) using a regression based on all PWS hatchery fish sampled from all locations and dates during 2001 and 2002 ($R^2 = 0.99$; $p < 0.001$):

$$W = 0.0000073 \cdot FL^{3.064}$$

Using back-calculated lengths and weights enabled us to track the average growth trajectories of known individuals rather than simply computing the mean monthly weights for juveniles sampled from open, mixed populations that could inflate variability due to a wider diversity of origins and growth histories. In addition, the latter approach is susceptible to potential bias from size-selective mortality or migration. By examining monthly frequency histograms of back-calculated size-at-circuli patterns, we determined that the hatchery fish sampled from each month displayed very similar growth histories, and could thus dismiss the concern about size-selective bias in the back-calculated growth estimates.

Moss et al. (2005) demonstrated that juveniles from the same hatchery cohorts that survived to adulthood were significantly larger than the average size of juveniles rearing in CGOA during their first growing season in 2001, and that significant size-selective mortality occurred after the first summer of life. To compare the feeding and growth performance of the average juveniles to those that survived to adulthood, we assumed that both groups of juveniles experienced similar thermal regimes and diet composition, but fed at different rates. For 2001, the back-calculated body weight of both the average juveniles sampled during summer 2001 and those for comparable life stages of the surviving adults were used in parallel simulations to estimate how much more food biomass and energy would have been required for the average juvenile to support the observed growth rate of the average survivor, assuming the same diet and thermal experience between groups (Table 1).

RESULTS

Generalized Bioenergetics Responses

An examination of the combined effects of weight- and temperature-dependent responses of the functions in the pink/sockeye salmon model (Beauchamp et al. 1989) provides insights into the physiological constraints facing Pacific salmon in the ocean under different environmental conditions (different thermal regimes, food availability and food quality). The specific rates ($g \cdot g^{-1} \cdot d^{-1}$) of both maximum consumption (C_{max}) and metabolic costs (basal and active metabolism) decline asymptotically with increasing body mass,

Table 1. Bioenergetics model inputs for simulations of the modal growth cohorts of hatchery pink salmon in Prince William Sound and Gulf of Alaska during the first spring-summer growing season. For 2001, the back-calculated body weight of both the average (Avg.) juveniles sampled during summer 2001 and those for comparable life stages of surviving adults (Surv.) were used in parallel simulations to estimate how much more food biomass and energy would have been required for the average juvenile to support the observed growth rate of the average survivor, assuming the same diet and and thermal experience between groups. Water masses refer to PWS = Prince William Sound; Trans = Transition Zone; ALL = PWS, Alaska Coastal Current and Trans.

Date	Day	Primary water mass occupied	BodyWt. (g)	Energy density (J/g)	Thermal experience	Small cope-pod	Large cope-pod	Euph-ausiid	Amphi-pod	Crab	Shrimp	Ptero-pods	Larva-ceans	Insect	Fish	Other
						Pink salmon					Diet composition (proportions by wet weight)					
2001			Avg., Surv.													
5/18/01	139	PWS	0.53, 0.53	4,102	8.0	0.00	0.74	0.05	0.00	0.02	0.00	0.04	0.00	0.02	0.04	0.09
7/11/01	193	PWS	8.4, 9.7	3,665	12.0	0.02	0.03	0.01	0.19	0.03	0.02	0.42	0.20	0.01	0.01	0.06
8/15/01	228	ALL	23.4, 28.2	4,134	14.1	0.02	0.26	0.09	0.33	0.06	0.01	0.08	0.01	0.04	0.02	0.06
9/19/01	263	Trans	51.1, 68.9	4,248	11.7	0.00	0.27	0.07	0.15	0.02	0.00	0.17	0.11	0.05	0.11	0.04
2002																
5/21/02	142	PWS	0.56	4,102	8.0	0.00	0.74	0.05	0.00	0.02	0.00	0.04	0.00	0.02	0.04	0.09
7/21/02	203	PWS	14.28	3,665	12.7	0.00	0.34	0.02	0.12	0.03	0.00	0.42	0.02	0.00	0.02	0.03
8/29/02	242	Trans	51.80	4,134	12.9	0.00	0.00	0.04	0.10	0.01	0.00	0.68	0.00	0.00	0.15	0.01

Table 2. Model inputs for the temporal change in energy densities (J/g wet weight) of the major prey taxa consumed by juveniles in Prince William Sound and Coastal Gulf of Alaska during spring-summer 2001 and 2002. Note that energy densities for "other" prey differ between 2001 and 2002 due to different diet compositions.

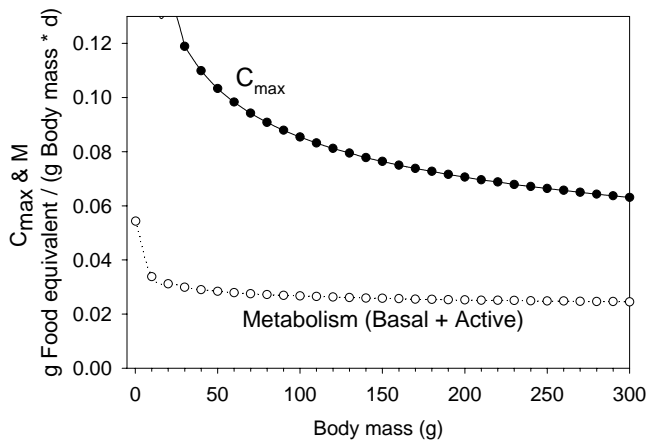|	Simulation days	Small copepod	Large copepod	Euphausiid	Amphipod	Crab	Shrimp	Pteropods	Larva-ceans	Insect	Fish	2001 Other	2002 Other
May-July	139-193	2,625	2,625	3,110	2,466	2,980	2,980	2,612	3,177	3,117	3,760	2,655	2,578
August	193-228	2,625	2,625	3,110	2,466	2,980	2,980	2,612	3,177	3,117	3,760	2,501	2,752
September	228-263	3,040	3,040	4,259	2,787	4,458	4,458	2,630	1,434	3,117	3,760	2,995	

Fig. 1. Weight-dependent functions for maximum daily consumption C_{max} and metabolic losses from basal and active metabolism. The curves are generated for sockeye salmon (0.3–300 g) at 20°C and represent specific daily rates of food consumption (g food eaten per g body mass per day) and the equivalent mass of food (with an assumed energy density of 4000 J·g^{-1}) needed to satisfy standard and active metabolic costs. The 20°C temperature represents the temperature where C_{max} is greatest for any given body mass.

but C_{max} declines more rapidly than metabolism (Fig. 1). For example, assuming a diet that averages 4000 J·g^{-1}, the metabolic costs for fry weighing 0.3 g represent 13% of the energy consumed at C_{max}, but metabolism rapidly increases to 21% of the energy in C_{max} for 10-g juvenile salmon and 51% for 1000-g salmon.

The energy budget of sockeye salmon changes considerably as a function of temperature as well (Fig. 2). When food is unlimited, the maximum consumption rate responds to increasing temperature as a dome-shaped curve. Waste losses and SDA are nearly constant proportions of consumption (Ney 1993), so the energy remaining after waste is subtracted from consumption also forms a dome-shaped curve in response to increasing temperature. Metabolic costs increase exponentially with temperature; therefore, the distance between the respiration + SDA line and the C_{max} – Waste lines represent the amount of energy remaining for growth (Fig. 2a). When plotting just the growth component of the energy budget under unlimited food conditions (Fig. 2b), growth potential also forms a dome-shaped response to temperature, and larger consumers (e.g., 100-g versus 10-g consumers) grow at slower rates in proportion to their body mass.

Fish do not frequently feed at C_{max}; therefore, we must consider how growth responds to temperature and other fac-
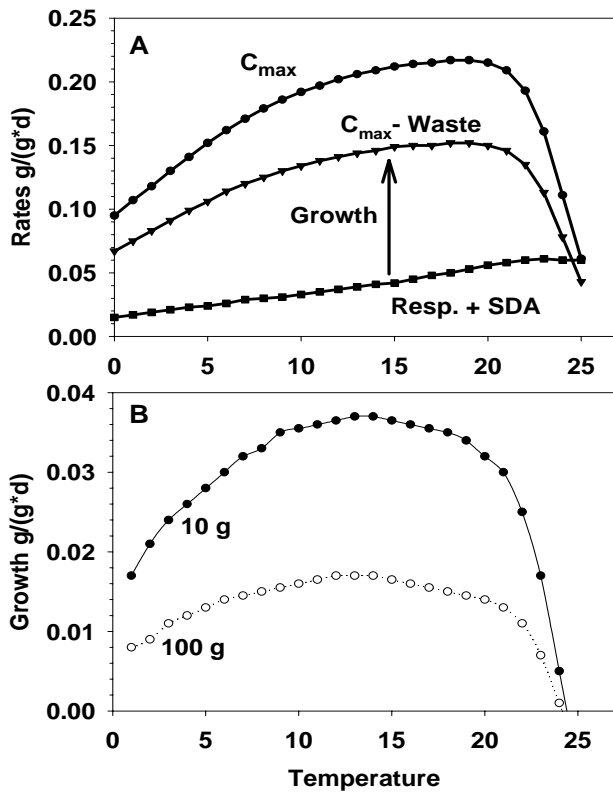
Fig. 2. A-Temperature-dependent functions for C_{max}, C_{max} – Waste losses, and Metabolic losses (Basal, Active, and SDA) for a sockeye salmon of any given body mass; and (B) a comparison of temperature-dependent daily growth rates between 10-g and 100-g sockeye salmon feeding at the theoretical maximum daily consumption rate C_{max} on prey containing an energy density of 2800 J·g^{-1}.

Fig. 3. A comparison of temperature-dependent daily growth rates for 10-g sockeye salmon feeding at different percentages of the maximum daily consumption rate C_{max} on prey containing energy density of 2800 J·g^{-1}, except the second lowest curve represents growth at 20% C_{max} with a diet containing high-energy prey (5000 J·g^{-1}). The maximum growth rate for each consumption level is indicated by G_{max}.

tors when feeding rates are considerably lower than maximum. Growth rates declined with reduced daily ration as expected, but the shape of the growth response to temperature also changed. As daily rations declined, growth was maximized at progressively lower temperatures (Fig. 3), and temperatures that permitted positive growth declined dramatically from 24°C at the maximum feeding rate, to 17°C when feeding at 20% of the maximum rate. For any given feeding rate, if the diet shifted from the normal mix of crustacean and gelatinous zooplankton with average energy density of 2800 J·g^{-1} to a higher-energy diet of squid, euphausiids, and fish, averaging 5000 J·g^{-1} (Aydin et al. 2005; Mazur et al. 2007), growth at the same feeding rate improved considerably (Fig. 3). Improved prey quality dramatically expanded the range of temperatures that could be tolerated at low ration sizes. For instance, at feeding rates of 20% of C_{max}, when prey energy density increased from 2800 J·g^{-1} to 5000 J·g^{-1}, growth rates more than doubled across all temperatures, and temperatures that allowed positive growth increased from 17°C to 22°C (Fig. 3). At higher feeding rates, higher prey energy densities increase growth rates disproportionately more than at lower feeding rates, but have much less effect on the range of temperatures that support posi-

tive growth. At higher rations, metabolic losses represent a smaller fraction of the total energy budget, so a larger proportion of the surplus energy from high quality prey can be converted directly into growth.

For any given feeding rate (constant *p*-value), growth remained within 10% of the maximum growth rate over a range of 11°C (8–19°C) at the maximum feeding rate and at the 50% feeding rate (5–16°C), but compressed to a 6°C range (4–10°C) at the 20% feeding rate. Outside these temperature ranges, feeding and growth rates declined at an accelerated rate. These results suggest that over a relatively broad range of temperatures and feeding rates, the direct thermal effects of climate change on growth are relatively minor, compared to the effects of differences in feeding rate or prey quality caused by climate-induced changes to the species composition and productivity of the water masses inhabited by salmon. However, outside those broad thermal growth plateaus, temperature becomes an increasingly important limit to growth, and the range of temperatures over which direct thermal effects become important will be strongly influenced by the effect of food availability on feeding rate (Fig. 3).

Juvenile Pink Salmon Simulations in Prince William Sound and Coastal Gulf of Alaska during 2001 and 2002

Higher growth and feeding rates were associated with 3-fold higher marine survival rates in 2002 compared to 2001 (Fig. 4A-C). Although growth and feeding were consistently higher during May–August 2002 than 2001, the biggest dif-

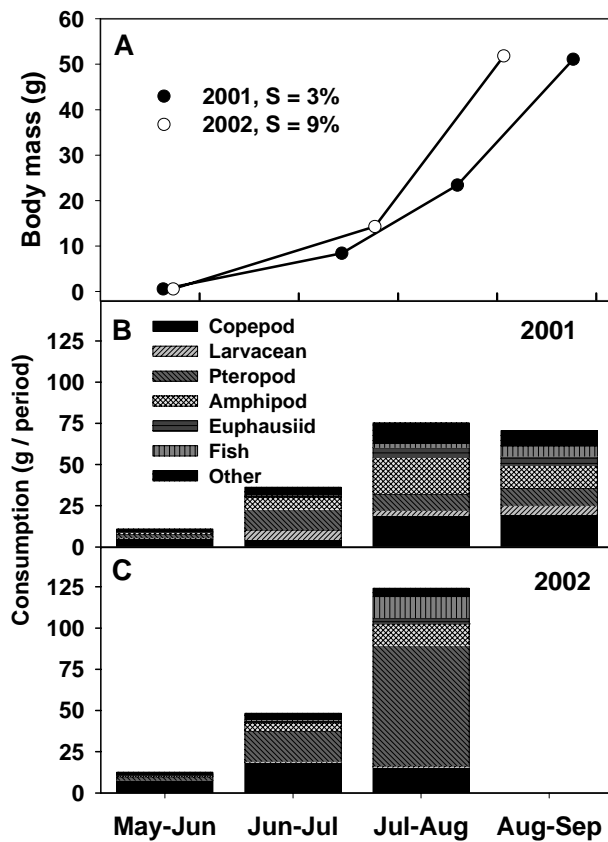**Fig. 4.** A. Comparisons between the back-calculated change in body mass of hatchery juvenile pink salmon over the initial growing season in Prince William Sound and coastal Gulf of Alaska during 2001 and 2002. The total estimated biomass of each major prey taxa consumed per 33-day simulation intervals during May-August in 2001 (B) and 2002 (C). An additional 20-day period was simulated in August-September 2001, because data were available.

ference occurred during July–August (Fig. 4A) and was associated with much greater consumption of pteropods (primarily *Limacina*) and more fish prey, but a lower biomass of hyperiid amphipods in 2002 compared to 2001 (Fig 4B,C).

In both years, feeding rates were initially lower in Prince William Sound during May–July, then increased through at least August. Feeding rates were at or near maximum consumption during this period in 2002 as suggested by p-values of 0.90–1.09 from the model simulations, whereas p-values of 0.79–0.83 (79–83% of maximum feeding rate) were estimated for simulations of May–August 2001 (Table 3). Temporal patterns of growth efficiencies (GE) were similar between years (GE = 25–31%), but GE was slightly higher during the fastest growth period in July–August 2002 (GE = 27%) than during 2001 (25%; Table 3). Temperatures differed during July–August between years, but were bracketed within the 12–14°C range (Table 3) where the direct growth response was insensitive to modest temperature swings of ±2–5°C when feeding rates were 50–100% of the maximum consumption rate (Fig. 3).

In order to directly compare feeding and growth performance between years, the total consumption of prey biomass and associated energy were examined for just the simulation days 142–242 that were common to both years during May 21 to August 29. Even though the average energy density of the composite diet was slightly higher in 2001 (2,739 J·g⁻¹) than 2002 (2,728 J·g⁻¹), the total mass of prey and associated energy consumed was considerably lower in 2001 (123 g, 336 kJ) than during 2002 (185 g, 505 kJ; Table 3). Therefore, prey availability and feeding rate were more important factors affecting growth rates between years than the differences in diet composition and associated energetic prey quality. The model simulations indicated that during summer 2001, juveniles that survived to become adults were 35% heavier and consumed 25% more energy than the average juvenile at the same life stages in CGOA (Table 3). However, even the survivors consumed and grew less than the average juvenile during the comparable simulation period in 2002.

DISCUSSION

Climate-forcing can directly or indirectly affect the distribution, feeding, diet, growth, and survival of Pacific salmon (Welch et al. 1998; Rand 2002; Kaeriyama et al. 2004; Mueter et al. 2005). The energetic responses of salmon provide a useful construct for mechanistically examining both direct thermal influence on metabolism and the indirect effects of climate-driven changes in the structure, function, and productivity of predator-prey assemblages within and among water masses. These energetic responses are expressed in terms of feeding rate and growth performance which in turn have consequences for survival during current or subsequent life stages.

The relative effects of feeding, thermal experience, and food quality on growth vary in complex, but predictable ways, based on species-specific, asymmetric responses of consumption and metabolism to changing body mass and temperature. Growth responses to temperature change were more pronounced for fish occupying marginal temperatures than for fish near the optimal growth temperature for a given feeding rate. Consequently, feeding rate or large shifts in prey quality would affect growth much more than a several-degree shift in temperature when near the optimal growth temperature, whereas temperature would become an increasingly important influence on growth if fish already occupied the cooler or warmer marginal temperatures. Moreover, temperatures and food supplies that might limit growth for older, larger life stages might not limit growth for smaller salmon. Thus, the energetic response to climate or ecosystem change could differ significantly among species and life stages of salmon because of their unique physiological responses to the thermal regime, their ability to utilize the available and exploitable food resources (based on feeding ontogeny), and how their time and energy budgets are affected by the localized density and distribution of prey, competitors, and preda-

Table 3. Results of the bioenergetics model simulations including proportion of the theoretical maximum daily consumption rate (P-value), total consumption C (g), growth G (g), growth efficiency (GE = G/C), and mean energy density of the diet (Diet energy density, J/g) over the simulation intervals. For direct comparison between years, total consumption in g and kJ, and average diet energy density are reported for a standardized period of simulation days 142–242 during both 2001 (juveniles and juvenile stages of surviving adults) and 2002. Water masses refer to PWS = Prince William Sound; Trans = Transition Zone; ALL = PWS, Alaska Coastal Current and Trans.

Initial date	Final date	Initial Julian day	Final day	Primary water mass occupied	Initial Wt	Final Wt	P-value	C	GE	Diet energy density	Initial temp.	Final temp.
2001	Average juveniles											
5/18/01	7/11/01	139	193	PWS	0.53	8.4	0.79	25	31%	2,891	8.0	12.0
7/11/01	8/15/01	193	228	PWS-All	8.4	23.4	0.83	59	25%	2,708	12.0	14.1
8/15/01	9/19/01	228	263	All-Trans	23.4	51.1	0.83	109	25%	2,723	14.1	11.7
Std. period 2001:		142	242					123		2,739	(Total 336 kJ)	
2001	Surviving adults											
5/18/01	7/11/01	139	193	PWS	0.53	9.7	0.84	29	31%	2,891	8.0	12.0
7/11/01	8/15/01	193	228	PWS-All	9.7	28.2	0.89	72	26%	2,708	12.0	14.1
8/15/01	9/19/01	228	263	All-Trans	28.2	68.9	0.98	155	26%	2,723	14.1	11.7
Std. period 2001:		142	242					154		2,739	(Total 421 kJ)	
% increase compared to average juveniles in 2001:						35%		25%			25% kj	
2002												
5/21/02	7/21/02	142	203	PWS	0.56	14.3	0.9	45	30%	2,747	8.0	12.7
7/21/02	8/29/02	203	242	PWS-Trans	14.3	51.8	1.09	140	27%	2,669	12.7	12.9
Std. period 2002:		142	242					185		2,728	(Total 505 kJ)	

tors. The ecosystem response to climate change will affect the species assemblage and density of food, competitors, and predators which will affect feeding rate, prey quality, and duration of foraging activity. Significant shifts in daily feeding rate or prey quality will always measurably influence growth performance at any temperature, whereas the direct effects of temperature change only become important to growth as ambient temperature deviates further from the maximum growth temperature for a given feeding rate.

Hatchery pink salmon from Prince William Sound exhibited higher feeding, growth, and ocean survival for juveniles inhabiting CGOA during 2002 than in 2001. Using bioenergetics model simulations, we determined that a higher feeding rate was the primary mechanism for improved growth during 2002, rather than because of changes in thermal regime or prey quality. Inter-annual temperature differences had little effect because all changes occurred within the relatively flat plateau at the top of the temperature-dependent growth curve. Inter-annual diet shifts resulted in a minimal change in energy density of the composite diets between years. Although a similar suite of prey groups appeared in the diet both years, the primary prey shifted from predominantly crustaceans during the low-survival year in 2001 (Hyperiid amphipods and copepods) to predominantly pteropods (*Limacina* spp.) in 2002. These significantly higher feeding rates suggested that the biomass of pteropods was considerably higher in CGOA during 2002. Higher proportions of *Limacina* spp. in the diet were also reported during August

1999 and 2000 (Armstrong et al. 2005), and were also associated with higher ocean survival rates. The dietary importance of gelatinous zooplankton like pteropods and larvaceans, especially the apparent correlation with higher growth and survival of pink salmon deserves further attention. Although the energetic quality of these gelatinous zooplankton is slightly lower than crustacean prey, when oceanographic conditions permit, their apparently high densities in the shallow (0–10 m) epipelagic layer during daylight support near maximum consumption rates without measurably sacrificing growth efficiency. Temporal-spatial responses of pteropods and other gelatinous zooplankton to climatic shifts and correlations with oceanographic conditions have been reported recently (Coyle and Pinchuk 2005; Zamon and Welch 2005). However, a closer examination of the seasonal dynamics and vertical density distributions of these prey and crustacean zooplankton during daylight, especially in the upper 10 m layer, will be needed before mechanistic links can be quantified between biophysical processes affecting exploitable zooplankton and salmon feeding, growth, and survival. An initial investigation suggests that routine zooplankton sampling methods severely underestimate densities of pteropods and other zooplankton that overlap with the depths of foraging salmon during daylight (L. Haldorson, unpublished data).

Understanding the mechanisms behind interannual differences in growth performance is particularly important, because stage-specific size-selective mortality appears to play

a significant role in regulating marine survival of salmon (Beamish and Mahnken 2001; Beamish et al. 2004). Moss et al. (2005) demonstrated that juveniles that survived to adulthood were significantly larger than the average size of juveniles rearing in CGOA during their first growing season in 2001, and that significant size-selective mortality occurred after the first summer of life. The model simulations indicated that surviving adults were 35% heavier and consumed 25% more energy than the average juvenile at the same life stages in CGOA during summer 2001. Thus, average feeding and growth performance during 2001 was substantially lower than was necessary for survival through subsequent life stages. As data become available, these analyses can be extended to more years, enabling a mechanistic examination of how different factors potentially contribute to temporal-spatial feeding, growth performance, and survival patterns among years and in response to climate and ecosystem variability. We might discover that different processes drive trophic dynamics and survival rates under different climatic and oceanographic conditions.

When closely coupled with a directed sampling program, bioenergetics modeling can help identify and quantify the major factors contributing to the growth rates observed and the rates needed to improve survival under a variety of oceanographic conditions. If food limitation, as indicated by lower feeding rates, is the primary cause, then we can focus on the relative importance of climate-forcing effects versus competition by hatchery fish or other species on ocean carrying capacity (Cooney et al. 1998; Hilborn and Eggers 2000; Wertheimer et al. 2004). The delayed size-selective mortality scenario described by Moss et al. (2005) allows more consumers to live and feed through the summer, thus depleting more of the food supply, reducing per capita growth, and mutually contributing to more severe size-selective mortality after the growing season. This size-selective over-winter mortality scenario imposes much greater consumption demand on ocean carrying capacity than either an acute, high initial marine mortality scenario or a constant mortality rate scenario. The latter two scenarios would both substantially reduce the consumer population before or during the first growing season, thus reducing prey depletion and enabling higher per capita feeding rates for the remaining consumers.

Data on spatial-temporal heterogeneity in temperature, prey availability, and prey quality can also be synthesized with bioenergetics models or linked foraging-bioenergetics models into a time series of maps displaying the distribution of high or low growth regions (Brandt et al. 1992). Spatial-temporal patterns in growth potential can then be compared to the distribution, growth performance, and survival of salmon during specific life stages as a bioenergetically-based application of the ideal-free distribution theory (Hughes and Grand 2000) to salmon in the ocean. Climate-induced shifts in seasonal ocean distribution patterns (Welch et al. 1998) could also be examined or predicted in terms of bioenergetic responses to the net effects of thermal conditions and food

supply. Welch et al. (1998) reported sharp upper thermal boundaries in ocean distribution patterns of sockeye salmon, but that these limits shifted monthly. The authors developed a bioenergetics-based conceptual argument for the sharp thermal boundaries, based on temperature-dependent responses of basal metabolism and maximum consumption. Their approach could be developed further by explicitly incorporating the effects of body size, activity costs, and feeding rate or food supply. Recall that as body mass increases, metabolic costs represent an increasing fraction of maximum energy intake. Therefore, older and larger life stages of salmon will have lower scope for growth or activity than younger, smaller salmon across all temperatures. Larger salmon should respond more sensitively to reductions in food supply or prey quality, because the temperatures that support the maximum possible growth rate (or even just a positive growth rate) for a given feeding rate should decline more rapidly than for smaller consumers as feeding rates decline. Therefore, bioenergetics modeling can provide a mechanistic framework for diagnosing and potentially predicting the effects of climate-induced changes in thermal regime and ecosystem productivity and structure on salmon distribution, production, and survival.

Despite broad acceptance and application of bioenergetics models, they should be used cautiously, and the objectives of model applications should be consistent with the capabilities for which they were originally developed. For many species, including Pacific salmon, parameters have often been "borrowed" from other species (Ney 1993), or constructed opportunistically from existing data sets that were generated for entirely different purposes.

As demands for more predictive models increase, bioenergetics-based models will need to be modified and refined to ensure that modeling capability can satisfy these expectations appropriately. Bioenergetics models have historically been used most effectively in a diagnostic or hind-casting role: predation impacts, food limitation, or thermal restriction would be simulated, based on existing data, to quantitatively diagnose which factors limited production, and then these results would be used to infer how similar scenarios applied to current and future conditions. To become more predictive, bioenergetics models need to link with complementary models that address important factors like behavioral shifts in movement, distribution, and feeding (e.g., migration or foraging models), variable activity costs, seasonal and ontogenetic energy allocation, and energetic feedbacks due to disease or environmental stressors. Potential modifications and complementary models are developing rapidly for environmentally- and behaviorally-driven foraging models (e.g., Stockwell and Johnson 1999; Hardiman et al. 2004; Mazur and Beauchamp 2006), feeding-migration models (Rand et al. 1997; Walters et al. 1997; Nottestad et al. 1999), and others. Existing bioenergetics models respond explicitly to temperature, but other important environmental factors should be included like salinity, dissolved oxygen,

and perhaps changes in physiological responses like growth compensation and seasonal or ontogenetic energy allocation.

The most contentious issue surrounding bioenergetics models for salmonids centers around the accuracy of functions for active and standard metabolism (Boisclair and Tang 1993; Trudel et al. 2004; Trudel and Welch 2005); therefore, some important advances in bioenergetics models for salmonids would be refinements to the functions for total metabolism (basal [standard] + activity). Trudel and Welch (2005) empirically derived and tested models for standard, active, and total metabolic rates for a wide range of body masses in both fresh water and salt water for sockeye salmon and steelhead. They determined that metabolic costs became increasingly biased as body mass increased, and that functions parameterized for one species did not necessarily perform well for even closely-related species. Because metabolism becomes an increasingly large fraction of the total energy budget for larger salmon, the implications of these results are particularly important for sub-adult and adult life stages (e.g., fish > 1 kg). For instance, if metabolism only represents 20% of the total energy budget (i.e., M + W + G) for a 10-g juvenile salmon, then a 40% error in M translates into an 8% error for estimates of either consumption or growth; however, if metabolism equals 50% of the energy budget for a 1-kg salmon, then a 40% error in M becomes a 20% error in consumption or growth estimates. For some modeling objectives, the magnitude of these errors might be perfectly acceptable, but for objectives that require very accurate and precise estimates for metabolism or other components of the energy budget, the application of some of the current models would not be appropriate.

Ideally, species-specific parameters would be generated from extended laboratory experiments involving factorial combinations of the body sizes and temperatures experienced by that species over its geographic range. Accurate daily measures of food intake (preferably using common prey types or reasonable surrogates), waste, and metabolic costs coupled with repeated measures of growth over multiple weeks or months of the experiment would be highly desirable. The consumption and growth experiments should be coupled with parallel factorial experiments to measure basal and active metabolism and SDA. In reality, the ideal experiments have never been accomplished, although some admirable subsets have been published recently (Madenjian et al. 2004; Bajer et al. 2004a, b). More of these experiments should be encouraged by management, research, and funding institutions.

Over the 15–25 years since the current bioenergetics models for salmon were developed, we have experienced major advances in and prevalence of physiological and positioning telemetry, hydroacoustics, remote sensing, respirometers, calorimeters, and other technologies, in addition to substantial increases in knowledge about the distribution, growth, trophic dynamics, and survival of salmon in fresh-water and marine ecosystems. These advances provide the opportunity to generate improved parameterized functions when necessary and to integrate currently disparate information and data in creative new ways. The table is set to advance our mechanistic understanding of salmon production ecology by synthesizing existing information with current models and other analytical tools, and by continued development of the promising avenues for improving existing models and linking with complementary foraging, migration, and behavior models.

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Comparison of Sockeye Salmon (*Oncorhynchus nerka*) Monitoring in the Fraser River Basin, British Columbia, Canada and Bristol Bay, Alaska, USA

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Abstract: We assess the quantity and quality of sockeye salmon (*Oncorhynchus nerka*) monitoring in two regions in North America (Fraser River, British Columbia and Bristol Bay, Alaska). We classify monitoring into two discrete types: that of a "parent" metapopulation (Tier 2), and individual populations (Tier 3). Effort within the Fraser River is focused more intensively at Tier 3, and consists of methods that provide relatively accurate counts of spawners. The monitoring in Bristol Bay is comprehensive and robust at Tier 2. While Tier 3 monitoring occurs throughout Bristol Bay, it is mostly in the form of aerial surveys, which provide less accurate estimates of spawner abundance. A rich set of data exists from visual ground surveys at Tier 3 in the Wood River, Alaska, drainage, but these data have not been analyzed to address population persistence, and there is a clear gap in reliable data on individual populations inhabiting the other major drainages in Bristol Bay. The overall level of monitoring efforts in the Fraser River basin, standardized to the amount of salmon spawning habitat, is conservatively four times higher than that currently expended in Bristol Bay. We encourage investments in continued monitoring and assessments of individual populations in the Wood River drainage, and recommend expanding efforts to include population scale monitoring in other drainages within the Bristol Bay region.

Keywords: sockeye salmon, Bristol Bay, Fraser River, monitoring, escapement

INTRODUCTION

Salmon monitoring often focuses on large, managed stock units that may be inappropriate to capture important biological phenomena that are critical for sustaining salmon productivity. The risks to small, unproductive stocks in mixed-stock fisheries have been known for a long time (Ricker 1973), and there has been increasing concern about the loss of these smaller populations in both British Columbia and the US (Walters and Cahoon 1985; Nehlsen et al. 1991). Loss of individual populations that make up these larger, exploited stock units may constitute a threat to sustainable fisheries (Ricker 1973; Hilborn et al. 2003).

One of the hallmarks of sustainable fisheries management is the establishment of safeguards to avoid overexploitation at the scale of these individual populations. Such individual populations underpin the larger, managed stocks that are the focus of modern fisheries management. Con-

cerns about conservation, embodied in endangered species legislation in both the US and Canada (e.g. see Ford 2004 for US; Irvine et al. 2005 for Canada), have led to concerted efforts to examine population persistence and extinction risk, and the development of approaches to manage fishing activities in ways that protect "weak stocks" or populations that exhibit low levels of abundance or productivity. This is accomplished through a variety of means, including fishing effort reduction, gear restrictions, or time-area closures.

Improved monitoring is needed to assess the effects of fishing on small or less productive populations. Augerot (2005) concluded there have been disproportionately high losses throughout the southern range of salmon on both sides of the North Pacific. While this effort relied on some published trend data on certain stocks or populations, the assessment relied extensively on best expert judgment, rather than quantitative criteria, to assess extinction risk. Augerot (2005) also highlighted the challenges of conducting range-

wide assessments given the pervasive problems of limited and non-standardized data and difficulties accessing data.

The State of the Salmon Program was initiated in 2003 to provide quantitative information to address the limitations described above in assessing trends in salmon diversity, to more fully characterize salmon population status and viability, and to provide a sound basis for designing and implementing a range-wide Pacific salmon conservation strategy. The first step toward reaching the above objectives is the creation of a common framework or knowledge system to integrate the many facets of multi-party monitoring efforts: sample design, field sampling, data standardization and analysis, and data storage protocols (see www.stateofthesalmon.org). This process will help ensure that we reach valid inferences, provide a means to make analyses more transparent, and identify important gaps in our knowledge. This effort will provide metrics by which we can measure status and trends for salmon across a range of scales (from regional management groupings, to metapopulations, to reproductively isolated populations).

For purposes of the present paper, we provide a preliminary summary of the State of the Salmon Program, with a focus on a single species (sockeye salmon, *Oncorhynchus nerka*) in two regions in North America that harbor diverse and relatively abundant populations: the Fraser River basin in British Columbia, Canada, and the Bristol Bay region in western Alaska, USA. In this paper we characterize our overall approach to the Salmon Monitoring Data Inventory and investigate salient differences in monitoring approaches with regard to understanding status and trends of sockeye salmon in both regions.

METHODS

Background and Approach to Data Inventory

The State of the Salmon Program's North Pacific Rim Salmon Monitoring Inventory is underway throughout North America, and we expect to extend it to the Russian Far East and Japan in the near future. We have embarked on a range-wide inventory of anadromous Pacific salmon monitoring to (1) provide a consistent framework to describe and assess monitoring efforts and (2) identify data of known quality to conduct quantitative range-wide salmon status and trend assessments.

To make the project tractable, we developed a conceptual framework to identify, describe, and organize monitoring activities. Key to the success of this effort is to standardize information to facilitate accurate automated queries of the resulting database, while preserving enough metadata to characterize data quality and utility. Our approach is designed to be transferable and reproducible for all Pacific salmon species across their natural range. It is important to note that although some of the data and similar analyses have appeared in previous publications, our emphasis on classifying monitoring activities provides a unique perspective. Further, our intent in this paper is to demonstrate to the reader how the Salmon Monitoring Inventory framework will accommodate a broad array of salmon monitoring activities and facilitate comparison for an array of species.

There are two principle criteria for inclusion of activities in the inventory: 1) any resulting dataset that contains quantitative estimates of the following parameters – abundance, distribution, diversity and productivity, and 2) the resulting data are of known quality, typically revealed by an adequate description of targeted life stage and methods or protocols used in data collection. For the purposes of the present paper, we focus on monitoring activities with the explicit objectives of documenting intra-specific diversity (at the genotypic and phenotypic levels, as revealed by molecular genetic techniques and standard biological sampling involving age, sex and length determinations), the distribution of the species in each region with respect to the migration corridor and spawning grounds, and abundance by life-history stage (juvenile, smolt and migratory adults during the spawning period).

Each monitoring activity included in our data base was geo-referenced and assigned a unique monitoring method, and the location and method of monitoring was used to classify each activity into a Monitoring Tier. The Monitoring Tier classification is a hierarchical schema that addresses the fit of a monitoring effort within one of three levels of biological organization: regional grouping (Tier 1), metapopulation (Tier 2) and population (Tier 3). While Tier 1 monitoring is still a common approach in regions throughout the North Pacific, this level of monitoring is not used for the post-season assessment of status for sockeye in our two focal regions. Tier 2 is meant to represent a group of populations that have likely undergone some degree of regional adaptation, or have a shared, unique ancestry. For the purposes of this paper, we relied on location and method of monitoring for Tier classification. In general, Tier 2 monitoring for sockeye salmon occurs in the lower river, using gear intended to enumerate fish across a larger river channel where it is likely that individuals from different populations are encountered. Conversely, those monitoring activities conducted in smaller river systems or lake beach areas that are in close proximity to the spawning grounds were considered Tier 3. Tier 3 monitoring activities are intended to assess more discrete, reproductively isolated populations. While fisheries agencies strive to define managed "stocks" that represent a natural grouping, these definitions are not universal. Our Tier schema is intended to overcome this problem and impose a common classification that is based on more fundamental, biological criteria. In this paper, we will refer to our Tier classes by number, and assess coverage or intensity of monitoring at the scale of drainages.

Sockeye are managed differently in Bristol Bay than in the Fraser. Drainages in Bristol Bay correspond to discrete management units. Within the Fraser River watershed four

run-timing groups constitute separate Management Units (Early Stuart, Early Summer, Summer, and Late). Within each Management Unit are 30–50 individual "stocks" or "populations" (Schubert 1998). Under Canada's Wild Salmon Policy (DFO 2005), biological status will be assessed and categorized for several hundred largely independent lineages of wild salmon (Irvine and Riddell 2007).

Acquisition of Metadata and Analysis

Monitoring activities were identified for inclusion and their associated metadata developed from a combination of sources, including participants' knowledge, existing databases or inventories, and public information sources such as the published literature, electronic documents, and web sites. Agency staff were contacted for further information on appropriate activities and public documentation. Metadata were entered directly into a relational database or a spreadsheet. Queries were developed to search for metadata records, and output was used to develop geodatabases in ArcGIS.

For our analysis, we focused on three common monitoring objectives for both regions: genotyping (using DNA markers), biological sampling (typically including age, sex and length determinations), and abundance (typically fry, smolt and adult escapement enumeration activities).

For genetic baseline development, we restricted our analysis to those baselines established by the lead agency in the respective regions (Alaska Department of Fish and Game (ADFG), the Gene Conservation Lab for Alaska, the Canada Department of Fisheries and Oceans (DFO), and the Molecular Genetics Laboratory for British Columbia). These baselines consist of both microsatellite DNA and single nucleotide polymorphism (SNP) markers, representing the best available techniques for stock identification. To characterize the extent of sampling for the development of a genetic baseline for the species, we obtained information on sampling locations from each lab. For Bristol Bay, we obtained station location data, in the form of latitude and longitude positions, from Drs. Jim Seeb and Chris Habicht (ADFG Gene Conservation Laboratory, Anchorage, AK). We classified these sampling locations as sites that yielded genetic data that have been used in a peer-reviewed publication (19 separate locations confined to the Kvichak River drainage (Habicht et al. 2003), or more recent sampling where data have not yet been fully analyzed and published (C. Habicht, ADFG, pers. comm.). Further, we distinguished whether the samples were drawn from river spawning populations or lake beach spawning populations. Dr. Terry Beacham of the DFO Pacific Biological Station, Nanaimo, BC, identified the sockeye stocks and/or populations for which genetic data have been obtained. Through consultations with Federal and Provincial biologists, we determined the approximate coordinates for the location of each of these units. With the exception of the Cultus Lake population, we assumed all populations

included in the Fraser River baseline were from river spawning populations, recognizing there are other beach spawning populations.

We identified the number of monitoring activities involving biological sampling for fry, smolts and adults (typically involving age determination using either scales or otoliths, sex determination and length measurements). For this analysis, we do not consider method of capture for biological samples. Because the quality of the abundance estimates for fry, smolt and adult escapement enumerations depend on method, we conducted analyses separately for each dominant method used in each region. For enumerating fry, we identified four methods: lake sonar, river fry trap, tow net, and beach seine sampling. The following methods were identified for monitoring smolts: traps, river sonar and fyke nets. For adults, the following methods were recognized: counting towers, sonar, bank-side visual surveys, mark-recapture, fences, and aerial counts. For the present paper, we do not consider monitoring efforts involving test fishing or harvest.

To examine temporal trends in monitoring efforts, we executed a query identifying the number of on-going monitoring activities by year during 1956–2005 for adult escapement in Bristol Bay (monitoring effort in the Fraser basin has been more consistent than in Bristol Bay). To describe monitoring effort in a consistent way over time, we examined trends separately for two types of activities: the number of aerial survey locations and the number of ground, visual survey locations. This provided an estimate of activities by year for each monitoring agency (ADFG and the University of Washington Alaska Salmon Program (UW). At present, the database identifies those activities that are not continuous during the period of record, but missing years for each activity have not been recorded in a standardized way. Hence the results of our query reflect the total number of activities recognized by the lead agency in each region as on-going by year, even though certain activities may not be repeated each year in the time series. Therefore the number of sites monitored each year represents a maximum number that may not reflect the actual number of sites sampled in any given year. For the purposes of this analysis, our intent was to determine whether any gross changes have occurred in monitoring effort throughout the period.

Metadata results were exported to ArcGIS. The first step was to create spatial data layers for the drainages that support ADFG and DFO managed sockeye stocks. We grouped drainages into areas sharing a common stock name associated with individual monitoring activities. For this exercise we used the BC Watershed Atlas for the Fraser River basin and an edited version of Hydro-1K, a dataset from EROS Data Center, for Bristol Bay.

Fish distribution spatial data layers for both regions were obtained and edited to reflect spawning river segments for sockeye salmon. The Bristol Bay data were provided by ADFG (reg05swt.shp, January 2005). This spatial data layer

was associated with a point file at a scale of 1:63,360 from ADFG's Fish Distribution Database Atlas and Catalog (Atlas and Catalog) indicating life stages that utilized the habitats. From these data the sockeye spawning habitats were identified for each stock in each region. Some minor editing was done to associate the lines with the appropriate stock. The Atlas and Catalog included both the migratory river corridor and the segments containing the spawning gravel as important for spawning. For the present analysis, we were interested only in identifying those segments directly supporting reproductive activities. Through consultation with ADFG area managers, we defined the spawning habitat as those segments above the downstream limit for spawning, which was typically waters draining into a nursery lake, excluding the river segments downstream of the lake outlet. Because we were not able to identify beach spawning habitat within rearing lakes in Bristol Bay, we simply identified rearing lakes in each drainage. The Fraser River data are represented by an ArcInfo spatial data layer called the FISS Sockeye Distribution Zones at a scale of 1:50,000. This data set demarcates the upper and lower points of stream segments used for spawning. This data set, completed in October 2002, was provided by DFO. It required some additional editing to remove overlapping lines. We also did not have a coverage identifying beach spawning areas in the Fraser River basin, so we identified those lakes that are thought to support beach spawning populations.

We classified all juvenile and adult monitoring by method and Monitoring Tier. Juvenile enumeration and biological sampling were typically considered Tier 2. Fry observed in a lake typically originate from more than one spawning population. Exceptions include monitoring of fry and smolts from lakes where only one population is known to exist, or monitoring efforts focused on collecting fry using traps deployed in a single lake tributary.

We used the metadata to estimate coverage of adult salmon monitoring in each region. Two different types of monitoring were considered separately: 1) genotype sampling representing an assessment of extant salmon diversity, and 2) abundance estimation or enumeration, in conjunction with non-genetic biological sampling to represent diversity with respect to age, sex and size composition. The development of genetic baselines typically focuses on adults on the spawning grounds. We estimated coverage of each baseline as the number of sampling locations divided by the number of river kilometers designated as spawning habitat within each drainage. For this paper, we assumed all enumeration monitoring (with the exception of aerial surveys) was done in conjunction with biological sampling. There were some cases where biological sampling is conducted where no enumeration activities are carried out. We did not include these cases in our assessment of monitoring coverage. We estimated monitoring coverage in two different ways. For Tier 2 monitoring, we estimated coverage by dividing the total amount of spawning habitat (in river km) upstream of the

monitoring location divided by the total amount of spawning habitat within each drainage. These activities are best described as "enroute" monitoring, where fish are intercepted and their destination is uncertain. Monitoring at Tier 3 is typically conducted on, or in close proximity to, the spawning grounds. To estimate coverage for these activities, we estimated the number of monitoring activities divided by the total number of river kilometers designated as spawning habitat within each drainage. We estimated coverage separately for three general classes of methods: aerial (number of river reaches surveyed), ground (which includes number of river reaches visually observed and the number of fences operated), and mark-recapture (number of reaches for which a population estimate is generated). In the present paper, we did not estimate monitoring coverage for beach spawning habitat. For these activities, we simply identified the number of lakes that are surveyed routinely for beach spawners.

RESULTS

Fraser River

Intensity of sampling for the genetic baseline for the species in the Fraser River drainage was somewhat higher than that in Bristol Bay. The number of sites per drainage ranged from a high of 12 for the Lower Fraser, to a low of 1 site for the Bowron drainage (Fig. 1). The sampling coverage, expressed as a ratio of sites sampled to the total river km designated for spawning in the drainage, varied from a high of 0.14 sites·km^{-1} for the Seton-Anderson drainage to a low of 0.03 sites·km^{-1} for the Bowron drainage (Figs. 1 and 2 (top)). This baseline has been well established through publications, and plays an integral role in managing mixed stock fisheries in this region.

Because monitoring effort in the Fraser River drainage has been relatively constant, we relied on recent monitoring activities to depict coverage. All major populations (with the exception of those in the Pitt Lake drainage) are monitored at the Tier 2 level by a lower river sonar site located near Mission, hence the monitoring coverage is close to 100% (with the exception of the Lower Fraser stocks that include the Pitt Lake drainage, where coverage is estimated to be 91.4%, Fig. 3). However, there is much uncertainty associated with this monitoring stemming from difficulties in obtaining accurate counts on a stock-specific basis due to limitations of the use of sonar, particularly during periods when run timing groups mix in the lower river, and when significant upstream-downstream milling occurs.

Tier 3 monitoring of adults in the Fraser River basin consists of a combination of fence counts, bank-side visual surveys, boat and lake shoreline visual surveys, mark-recapture efforts, and aerial surveys (Fig. 3). These activities occur close to the spawning grounds and provide the data necessary to reconstruct abundance and are used, in combination with harvest data, to estimate exploitation rates for the
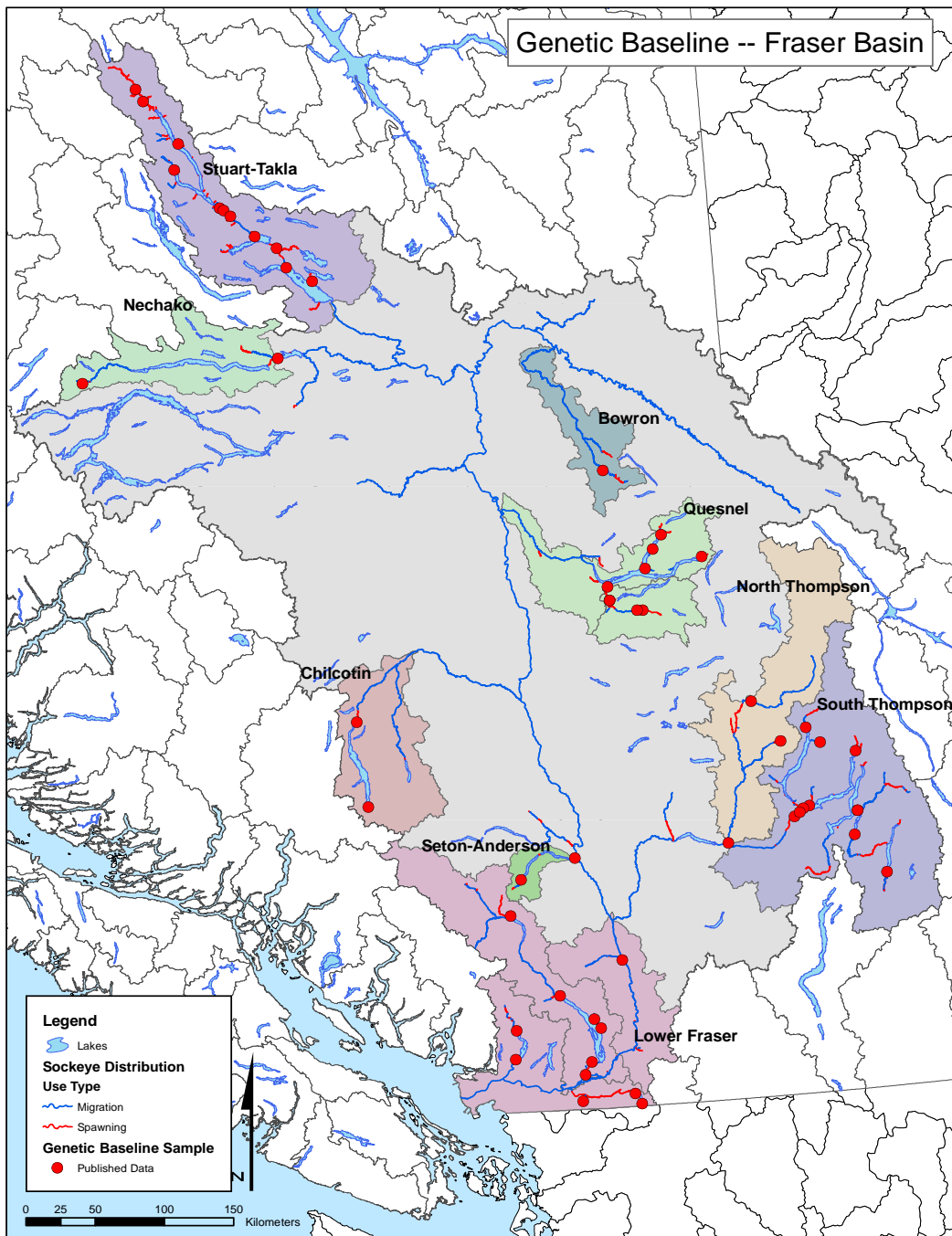
Fig. 1. Locations of samples contributing to the sockeye salmon genetics baseline within the Fraser River drainage maintained by Department of Fisheries and Oceans (DFO), Canada (Beacham et al. 2006).

major stock aggregates. The level of monitoring intensity, classified into our three general categories (aerial, ground and mark-recapture), varied within each drainage from a high of 0.08 to a low of 0.01 sites·km^{-1} (Fig. 4), excluding beach spawning survey effort. With the exception of three drainages (Chilcotin, North Thompson and Bowron), fences are used to enumerate adult escapement in the Fraser River basin, ranging from as many as four fence monitoring ac-

tivities ongoing in the Stuart-Takla drainage, to one in the Seton-Anderson and Quesnel drainages (Fig. 3). Bank-side visual surveys are routinely conducted in five of the drainages: Lower Fraser (5), North Thompson (4), South Thompson (13), Stuart-Takla (22), and Seton-Anderson (1). Boat and lake shoreline visual surveys targeting beach spawning populations are conducted in the Chilcotin drainage (Chilko and Taseko lakes), Lower Fraser (Harrison, Chilliwack and
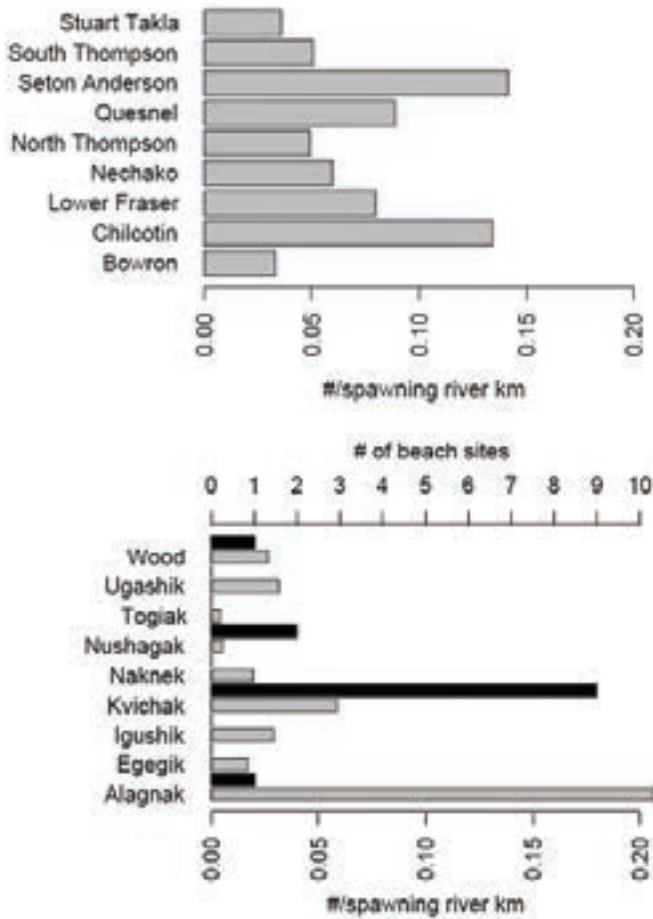
Fig. 2. Level of intensity of the sockeye salmon genetic baseline sampling for Fraser River (top panel) and Bristol Bay (bottom panel). The intensity level is measured as the number (#) of sampling locations divided by the total number of river kilometers for each stock designated for spawning use for river spawning populations. For lake spawning populations, the number of beach locations sampled per stock is presented. Grey bars in the figure represent river sites, and dark bars represent lake beach spawning locations.

Cultus lakes), Quesnel drainage (Quesnel Lake), and the South Thompson drainage (Shushwap and Adams lakes). Mark-recapture methods are applied to enumerate adult escapement in the Chilcotin, Lower Fraser, Quesnel, South Thompson, and Stuart-Takla drainages (Fig. 3). Aerial surveys are conducted in four of the drainages: Stuart-Takla, Nechako, Bowron and North Thompson (Fig. 3).

Juvenile monitoring of sockeye salmon in the Fraser River consists of a combination of lake tributary fry trapping, sonar and tow netting, and smolt trapping. Fry trapping is conducted routinely on three tributaries (Forfar and Gluske, two tributaries of the Middle River in the Stuart-Takla drainage, and the Stellako River, a tributary of the Nechako River, Fig. 3). These are classified as Tier 3 monitoring. Sonar sampling of lake fry, and associated tow netting, are conducted routinely in Cultus Lake (Lower Fraser drainage), Quesnel Lake (Quesnel drainage) and Chilko Lake (Chilco-

tin drainage) (Fig. 3). These activities were classified as Tier 2 monitoring, because individuals observed in these activities are likely to originate from more than one population. Smolt monitoring is conducted on the Chilko River (Chilcotin drainage, known to support multiple populations and, hence, classified as Tier 2 monitoring) and Sweltzer Creek, the outlet of Cultus Lake (Lower Fraser drainage, considered a single population and, hence, classified as Tier 3 monitoring (Fig. 3).

Bristol Bay

The genetic baseline for the species in Bristol Bay is being developed. We distinguish the sample locations that appear in Habicht et al. (2004) in Fig. 5 as published (restricted to the Kvichak River drainage) from the sites that have been sampled but await full analysis and reporting. We consider river and lake spawning populations separately for this analysis. The number of sites sampled for the baseline varied by drainage, with the greatest number of sites established in the Kvichak drainage (50 river sites and 9 beach sites, including both published and unpublished data) to the Togiak and Igushik sites, where 3 and 4 river sites were sampled, respectively (Fig. 5). Intensity of sampling at river sites varied from a high of 0.2 sites·km^{-1} for the Alagnak drainage to a low of 0.004 sites·km^{-1} for the Togiak drainage (Fig. 2 (bottom)). Beach sites were sampled in the Alagnak (1), Kvichak (9), Nushagak (2) and Wood River (1) drainages (Fig. 2 (bottom)).

We found a marked temporal trend in monitoring effort within Bristol Bay, indicating a peak in monitoring occurring in 1984, followed by a decline during the late 1980s (Fig. 6). This trend was driven primarily by a reduction in aerial surveys performed during peak escapement periods (Fig. 7). Here we examine characteristics of monitoring during a recent period (2000–2005), and later examine how effort has changed by explicitly contrasting present monitoring with an earlier period (1982–1986). It is important to note here that aerial surveys were discontinued by ADFG during 2001–2004, and were resumed in 2005 through a combined effort with UW. Here we include the amount of aerial surveys that took place during 2000 and 2005 to represent the period 2000–2005.

Our Tier 2 classification corresponds to the drainages recognized by ADFG as supporting separate managed stocks within this region, and the extent of coverage for Tier 2 monitoring reflects the interests of ADFG to monitor escapement at the metapopulation scale (ranging from 8–100% coverage by stock, mean = 76.8%, median = 82.5% (Fig. 8)). Tier 2 monitoring consisted mostly of tower counts below the main nursery lakes in each drainage in Bristol Bay (Fig. 8). An exception to this is the Nushagak drainage, where ADFG maintains a sonar enumeration site in the lower river, in addition to an upstream tower site. Coverage by tower counts was relatively low (11.7%) for Nushagak given its upstream
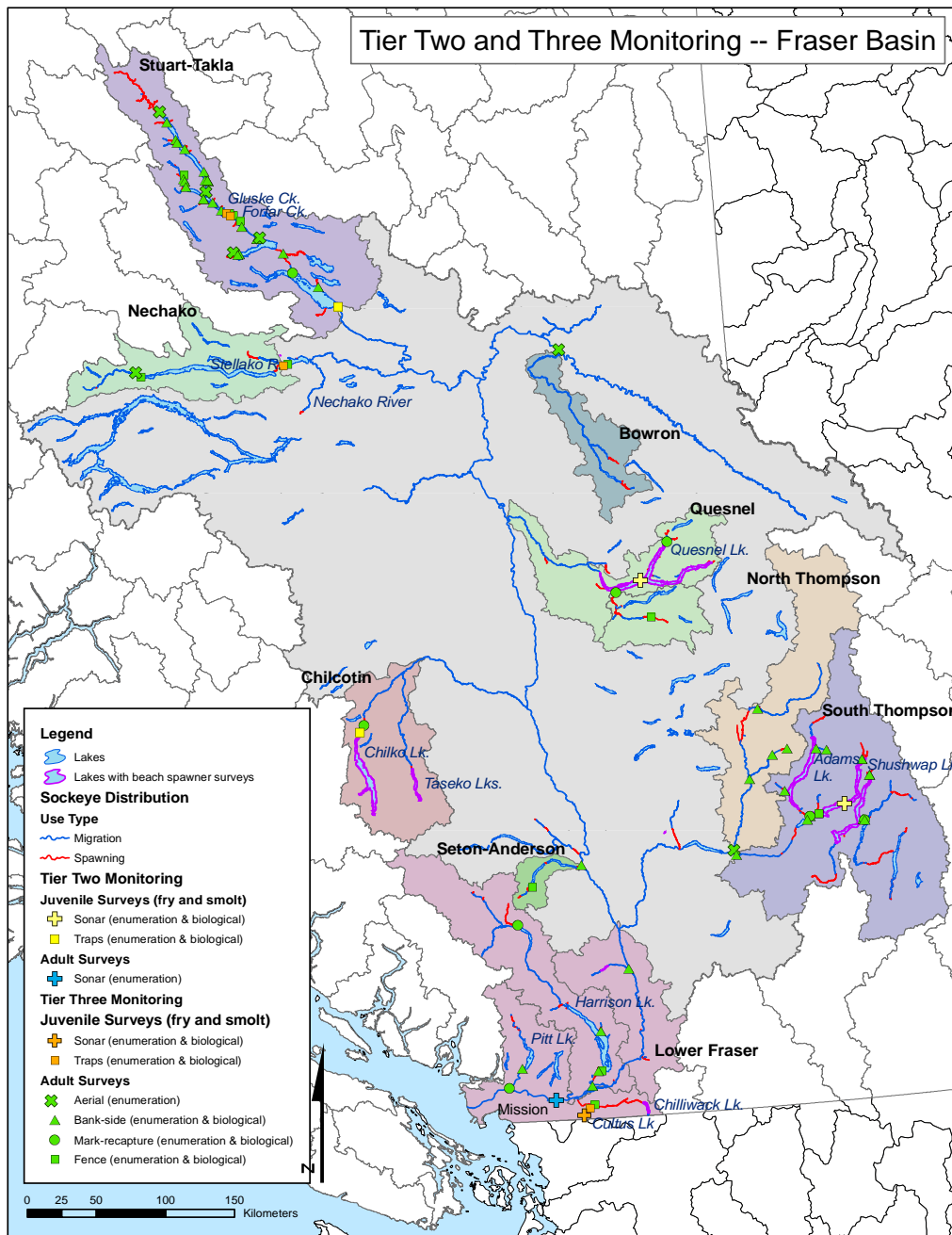
Fig. 3. Monitoring efforts for sockeye salmon currently considered ongoing in the Fraser River drainage by the Department of Fisheries and Oceans. Distribution of the species is indicated by usage type, migration (in blue) and spawning (in red). Lakes where beach spawning surveys are conducted on adults are highlighted. Monitoring is broken down by Tier (2 or 3), life stage (juvenile, smolt or adult), and monitoring objective (biological and enumeration). The major drainages supporting the managed stock units are depicted by colored polygons and identified by name.

position in the drainage (Fig. 8). Coverage at Tier 2 in the Togiak drainage was also low (7.7%) relative to the other drainages owing to the configuration of the watershed with numerous basins, each with separate ocean entry points (Fig. 8). An additional tower is maintained on the Newhalen River by the United State Geological Survey (USGS) to quantify escapement of sockeye to the Lake Clark system (Fig. 8).

Tier 2 sampling for juveniles in Bristol Bay consists of paired surface trawls in five of the Wood River lakes, providing estimates of relative abundance (CPUE) and biological data (Fig. 8). There are also a number of stations established for monitoring lake fry in the eastern portion of Lake Iliamna and in Lake Clark. Historically, smolt monitoring programs consisting of sonar (for enumeration) and fyke nets (for
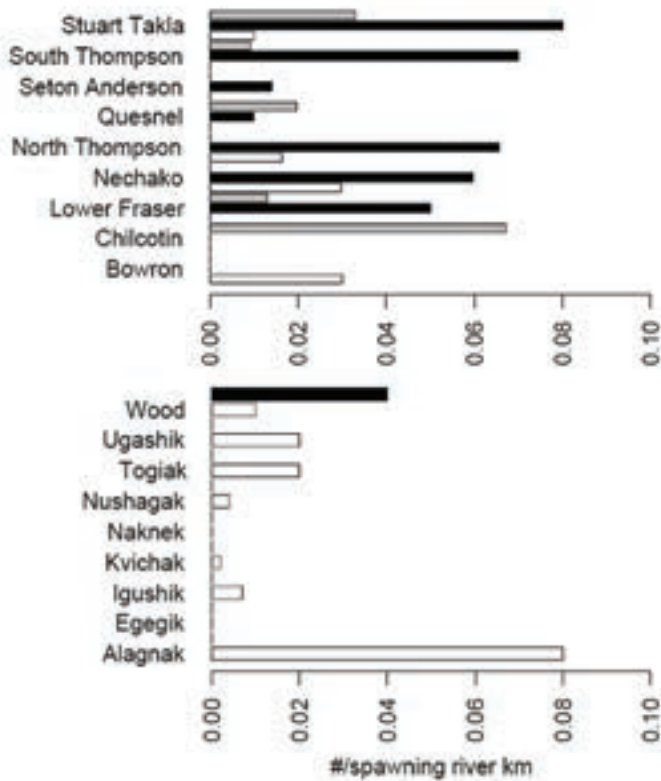
Fig. 4. Level of intensity of the sockeye salmon Tier 3 monitoring for adults for Fraser River (top panel) and Bristol Bay (bottom panel). The intensity level is measured as the number (#) of monitoring locations divided by the total number of river kilometers for each stock designated for spawning use. Open bars are aerial surveys, black bars are bank-side surveys (combination of bank-side visual surveys and fence counts), and grey bars are mark-recapture estimates of abundance.

biological monitoring) were active in six of the drainages (Wood, Nushagak, Kvichak, Naknek, Egegik and Ugashik). These programs were phased out during 1990–2002 (Crawford and Fair 2002).

We found that the finest resolved sampling effort (Tier 3, population scale) was performed in seven out of a total of nine drainages in Bristol Bay (Tier 3 sampling is lacking in Egegik and Naknek basins, Figs. 7 (bottom), 9). The Tier 3 sampling was accomplished mostly through aerial surveys in the seven drainages, with the exception of the Wood River, where monitoring was supplemented through ground, visual surveys (including biological sampling of age, sex and length) in a number of lake tributaries by UW personnel (0.04 sites·km^{-1}, Fig. 9). The Kijik River system, a tributary of Lake Clark in the Kvichak drainage, has also been monitored by USGS using ground, visual survey methods. The intensity of aerial surveys, conducted by ADFG, UW and USGS, was greatest for the Alagnak stock (0.08 sites·km^{-1}), followed by Togiak (0.02 sites·km^{-1}), Ugashik (0.02 sites·km^{-1}), Wood (0.014 sites·km^{-1}), Igushik (0.007 sites·km^{-1}), Kvichak (0.002 sites·km^{-1}), and Nushagak (0.0004 sites·km^{-1}) drain-

ages (Fig. 4). Only two sites were surveyed by air in the Kvichak during 2000–2005, representing an order of magnitude less effort relative to the other drainages (Fig. 7).

The drop in monitoring effort in Bristol Bay between the early and later period was driven primarily by a decrease in the number of sites surveyed using aerial methods (Fig. 7). The decrease was observed most dramatically in three of the drainages (Nushagak, Kvichak and Wood rivers, Fig. 7). Aerial survey coverage declined from a total of 36 sites (0.02 sites·km^{-1}) to one site (0.0004 sites·km^{-1}) in the Nushagak, 66 sites (0.08 sites·km^{-1}) to two sites (0.002 sites·km^{-1}) in the Kvichak, and 15 sites (0.02 sites·km^{-1}) to nine sites (0.01 sites·km^{-1}) in the Wood (Fig. 7).

DISCUSSION

Bristol Bay and the Fraser River represent the most productive regions for sockeye salmon in North America. While the total surface area in each of the two basins is similar, the rearing lake area in Bristol Bay is over four times greater than in the Fraser River drainage. Total production, described by the average number of sockeye returning to each region, corresponds to the differences in fry rearing habitat, with Bristol Bay receiving over four times the number of returning fish relative to the Fraser River in an average year (Table 1). Returns to many systems in the Fraser are cyclical, but even in high return years, Bristol Bay runs are larger.

In many ways, Bristol Bay and Fraser River sockeye monitoring programs represent the best-case scenarios for salmon status and trend monitoring anywhere across the North Pacific. These regions and their salmon populations have been studied more intensively than many others, largely due to their high commercial value. Fisheries on these populations are managed to minimize the risk of significantly over-exploiting the major stocks. However, recent declining trends for some stocks is cause for concern (e.g. the Kvichak stock in Bristol Bay, and Cultus Lake in the lower Fraser River basin). Clearly we do not want to experience losses in salmon diversity that may erode the ability of populations to persist over time. Further, there appears to be significant gaps in monitoring, particularly within Bristol Bay, that make it difficult to ascertain the true impact of continued harvest regimes on the overall viability at the scale of individual populations. The Wood River drainage is an exception, and recent initiatives by the UW will help assess how fishing pressure may have influenced these populations over time.

Our approach examines the spatial extent and data quality of monitoring implemented for stock assessment and conservation. Our larger goal for these studies is to allow a fully comprehensive comparison of status and trends for salmon across their natural range, and provide a means to gauge objectively the effectiveness of monitoring in each region with an eye on providing a safeguard to avoid irreversible loss of salmon diversity. The case study provided in
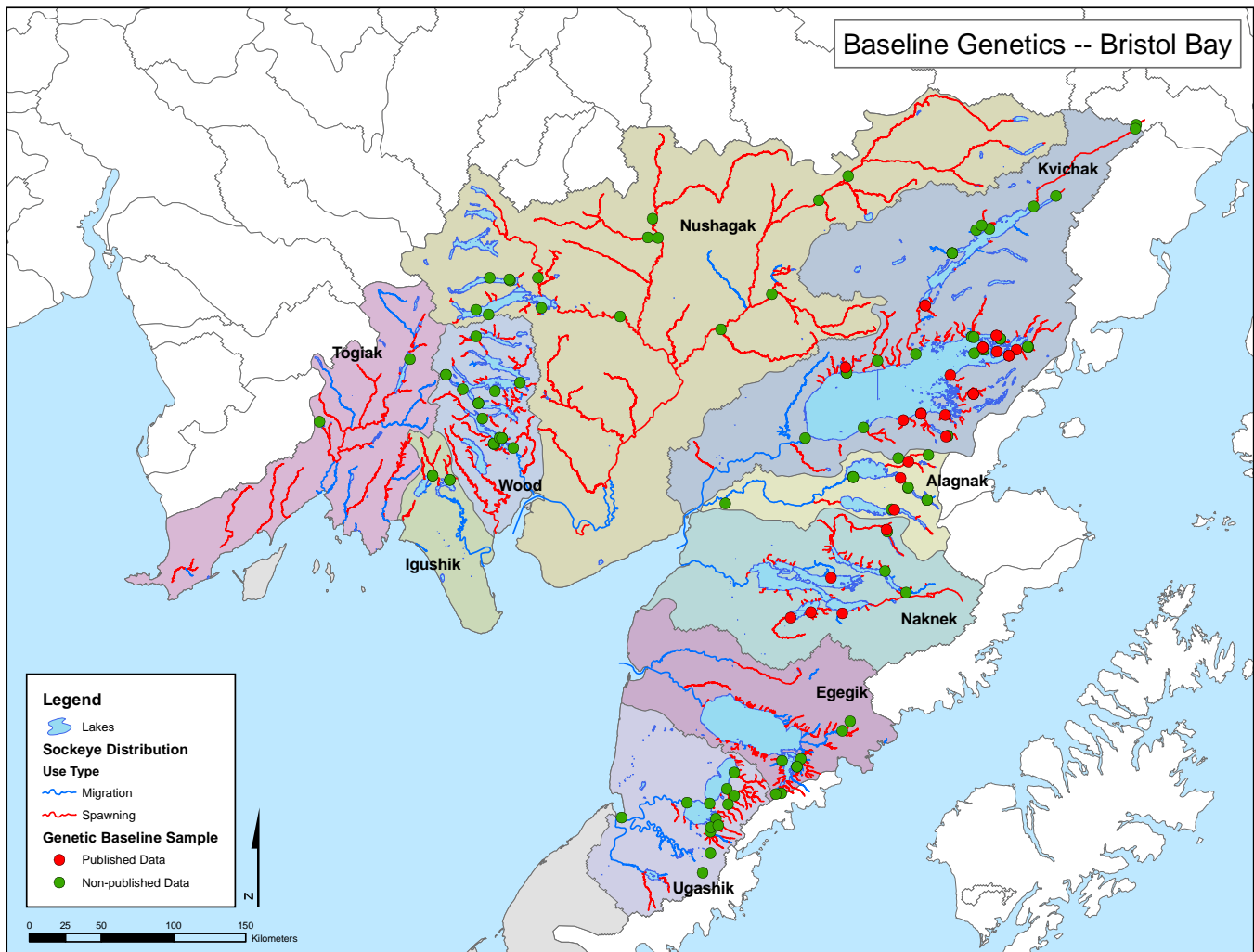
Fig. 5. Locations of samples that are included in the sockeye genetics baseline within Bristol Bay maintained by Alaska Department of Fish and Game. Data that have been published are identified with red circles (Habicht et al. 2004). Genetic data obtained from the other sample locations (indicated by green circles) are presently being analyzed (C. Habicht, ADFG, pers. comm.).

this paper is challenging for a variety of reasons, including the overall level of complexity in monitoring and management of the fisheries, participation by numerous agencies, the complex population structure within the managed sockeye salmon stocks, and the inevitable complications associated with making valid comparisons across two regions that differ in fundamental ways. Despite these challenges, our results underscore the value of closely examining the nature of monitoring activities that provide the data to conduct assessments of status and trends for stocks targeted by intensive, commercial fisheries. There has been a long history of overexploitation of marine fisheries leading to declines and extinctions (Botsford et al. 1997; Myers and Worm 2005). In much of the Bristol Bay and Fraser River drainages, in contrast to areas in the US Pacific Northwest, there have been relatively limited deleterious anthropogenic impacts on instream habitat (e.g., little or no impediments to migration

resulting from dam construction) and little hatchery introgression. There is an active hatchery program underway for Cultus Lake sockeye in the Fraser however, and there has been significant enhancement of sockeye salmon in other parts of the basin, mostly in the form of artificial spawning channels (Weaver Creek in the Lower Fraser, Gates Creek in the Seton-Anderson, Horsefly River in the Quesnel, and Nadina Creek in the Nechako). It appears that the greatest risks to sustainable salmon populations in these two regions are the mixed stock commercial fisheries targeting these stocks, as well as global climate change (Morrison et al. 2002; Cooke et al. 2004; Rand et al. 2006). Canada's Wild Salmon Policy proposes new management and assessment approaches in response to concerns about declining diversity (DFO 2005).

In both of our examples, agencies have identified declining trends in abundance of certain stocks and have imple-

Table 1. Physical attributes of the drainage basins compared in this study, with an estimate of the mean total return (catch plus escapement) of sockeye salmon during 1956–2005. Ranges provided for the Fraser River are intended to represent the physical gradient from the coastal rain forest climate to the arid conditions in the interior plateau.

Parameter	Bristol Bay	Fraser River
Mean January Temperature (°C)[1]	-9	-7 to 5.7
Mean Annual Precipitation (cm)[1]	57	27 to 246
Total Watershed Area (1000s km²)[2]	193	284
Sockeye Watershed Area (1000s km²)[2]	175	123
Sockeye Lake Area (1000s km²)[2]	14	3
Mean Sockeye Return (in millions)[3]	39	7.9

[1]Climate data was sourced from the Alaska Climate Research Center and the Fraser River Action Plan.
[2]Watershed area was obtained from spatial data layers described in text.
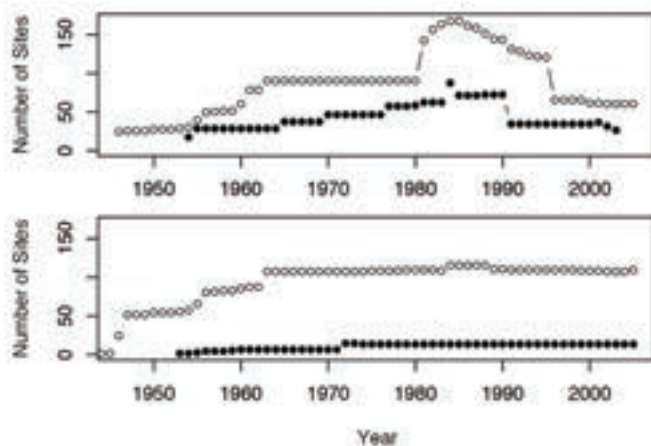[3]Mean returns (catch and escapement, 1950-2002) was obtained from ADFG and Pacific Salmon Commission.

Fig. 6. Level of monitoring effort over time (1946–2005) in the Bristol Bay drainage, Alaska, by method (top panel: aerial surveys; bottom panel: ground, visual surveys). Open circles are activities run by the University of Washington, and filled circles are activities run by the Alaska Department of Fish and Game.

mented changes to reduce harvest (Fair 2003; Irvine et al. 2005). Whether these measures will be effective at avoiding irreversible losses of salmon diversity remains to be seen. The key difference we observe between the two regions is that monitoring in the Fraser River is capable of tracking dynamics at a more finely resolved scale that approaches a population "unit" (our Tier 3 classification) characterized by reproductive isolation. In the context of Bristol Bay fisheries management, losses of individual populations could be occurring under present harvest regimes, but cannot be documented given the paucity of Tier 3 monitoring data. It is possible to examine status and trends at this scale in the Wood River system, and we encourage efforts to analyze these data to determine how natural and anthropogenic factors may have influenced population dynamics in this basin. Outside of the Wood River drainage, aerial surveys represent

the majority of Tier 3 monitoring in Bristol Bay, but are primarily used as a means to set overall escapement goals and are not explicitly linked with the development of life tables used to track current status of either individual populations or the overall managed stock. Further, these aerial survey programs have been cut back markedly in recent years.

A recent effort to examine trends in abundance in the Kvichak River drainage using aerial survey data concluded that there has not been a discernable loss in individual populations, or a shift in the relative contribution of individual populations to the larger Kvichak stock unit (Stewart et al. 2003). An important caveat of the study by Stewart et al. (2003), however, is that the data used in the analysis may be biased due to the fact that much of the monitoring (particularly those populations that were relatively small) after the late 1980s has been discontinued (this is clearly evident in our Fig. 7). It would be expected that these small populations would be disproportionately affected by an intensive, mixed-stock harvest regime. It appears that the beach spawning populations in the region represent the greatest contribution to peak cycle production, but these stocks appear to be much less productive in recent years. This argues strongly for closely examining shifts in stock structure within these larger managed stocks to help explain temporal trends in abundance. While we acknowledge difficulties (both financial and logistical) in carrying out more comprehensive monitoring, particularly in such a remote region, we conclude that this effort is extremely important to provide definitive information concerning the ability of individual populations to persist given the current harvest regime, and expected changes in habitat that may occur from land use and global climate change. We encourage monitoring approaches that balance the assessment of biological status with abundance and distributional trends for individual populations of varying size and productivity. Canada's Wild Salmon Policy describes such an approach (DFO 2005, pp.18–19), and another is the probabilistic survey design for coho salmon (*O. kisutch*) in coastal Oregon, USA (Stevens and Olsen 1999). Monitoring should be cost effective and yet provide robust inferences on the condition of individual populations that underpin larger managed stocks.

Our approach relies on a detailed assessment of spawning habitat in each surveyed region. We acknowledge a problem with our inter-regional comparison stemming from the different resolutions of "spawning habitat" identified for sockeye within each region by the lead agencies. The habitat for sockeye spawning is more finely resolved in the Fraser River drainage compared to Bristol Bay. Further, we were unable to assess monitoring intensity for beach spawning populations given the lack of data on the distribution of suitable spawning habitat within the main rearing lakes in the region. A more resolved mapping of spawning habitat extant in Bristol Bay would result in higher estimates of monitoring intensity than that reported in the present analysis. We recommend more concerted efforts at resolving spawning habi-
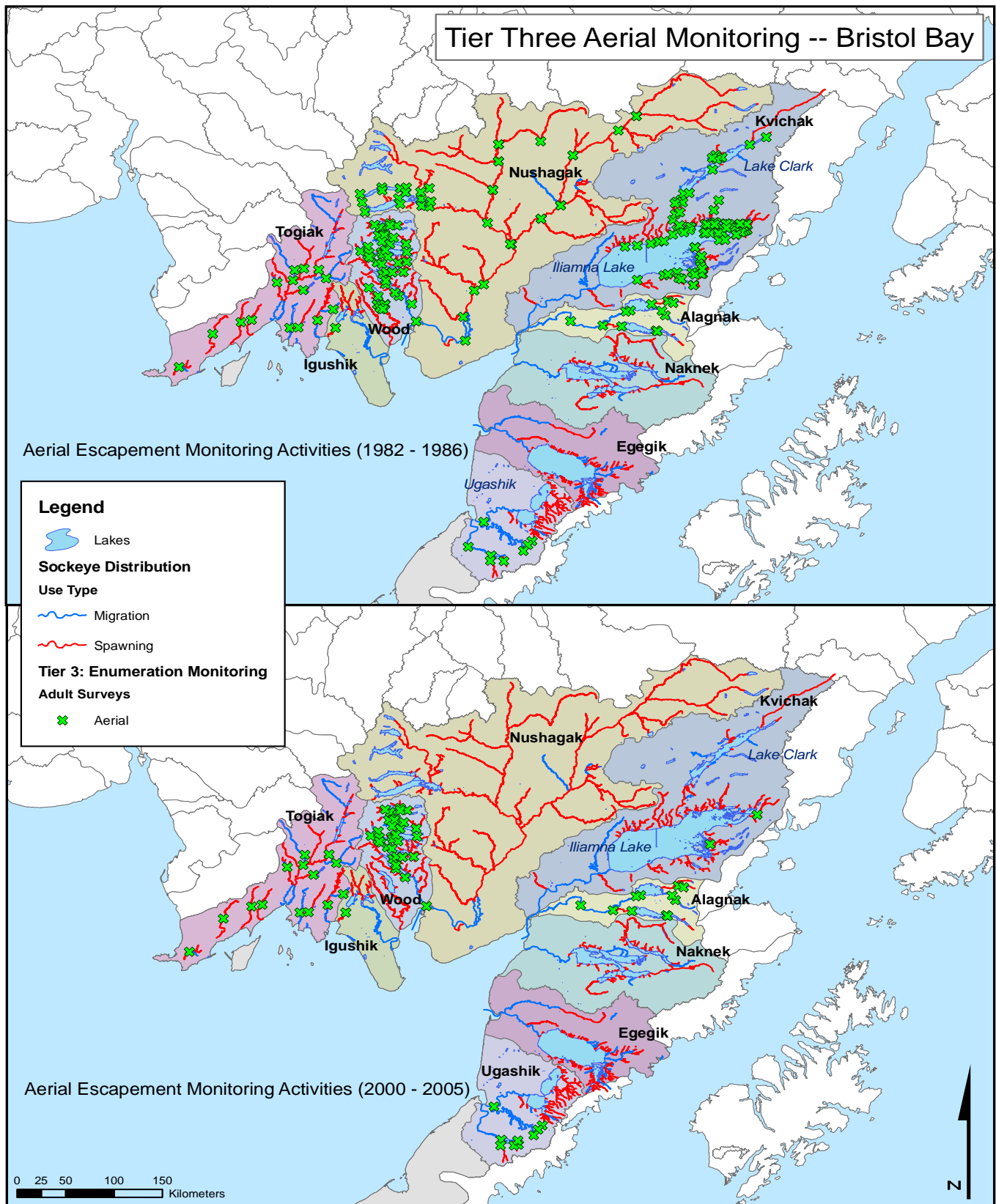
Fig. 7. Aerial monitoring activities designated as Tier 3 within the Bristol Bay drainage. Survey coverage is depicted for a period representing peak effort (top 1982–1986) and current effort (bottom 2000–2005). Note that the latter period included four years (2001–2004) during which no aerial surveys were conducted.
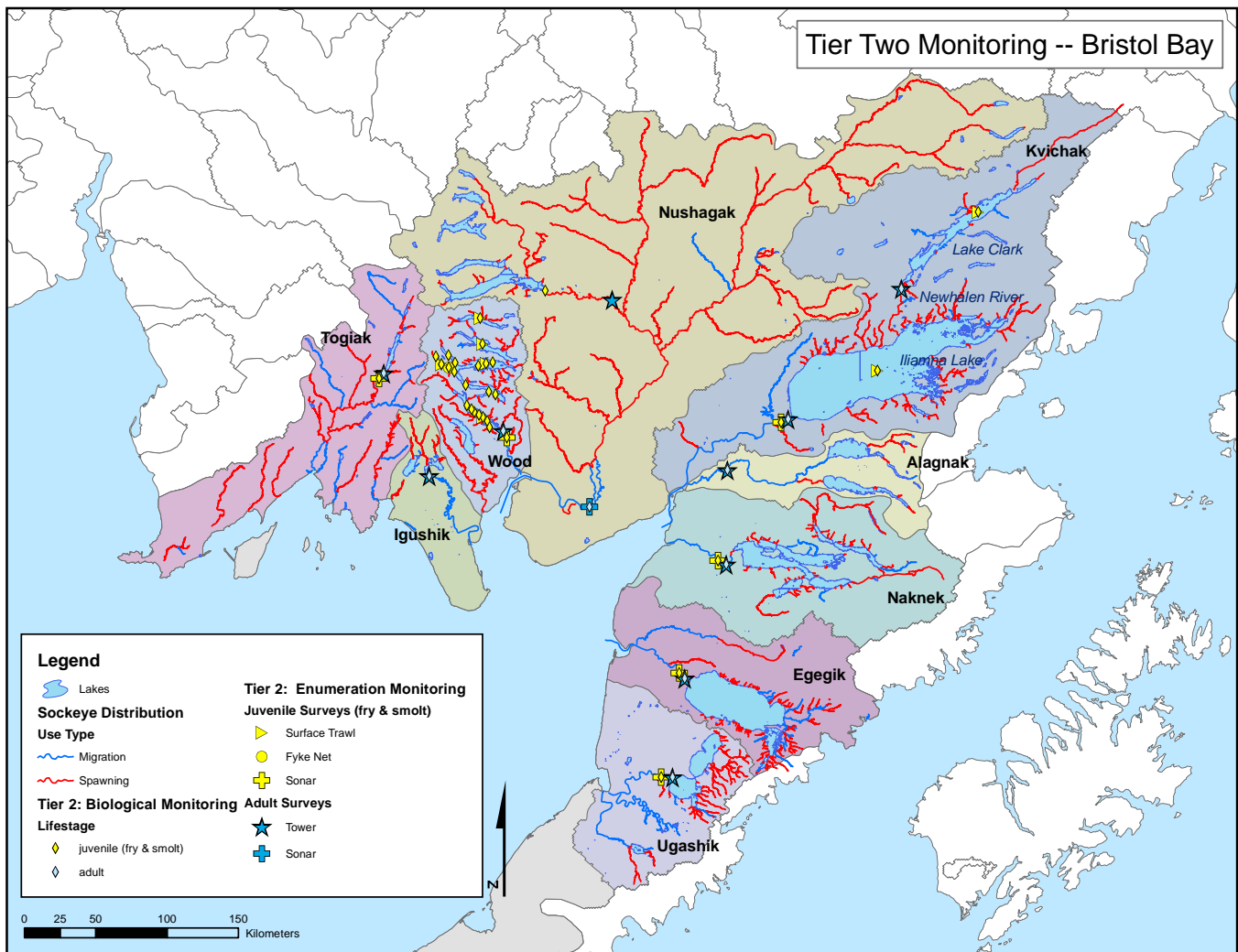
Fig. 8. Monitoring activities designated at Tier 2 within the Bristol Bay drainage. Monitoring activities are broken down by monitoring objective (biological and enumeration), life stage, and method. Distribution of the species is indicated by usage type, migration (in blue) and spawning (in red). This figure is meant to represent the total number of monitoring activities during 1982 to the present.

tat in this region. This may be possible by examining more closely the patterns of abundance of spawners through aerial surveys. Having a better understanding of the distribution of spawning habitat will be critical in the future as threats to spawning habitat are likely to increase.

The level of effort devoted to conducting a biological inventory of populations, accomplished through the development of a genetic baseline, were comparable for the two regions. While stock identification protocols are a fundamental component of sockeye fisheries management for the Fraser River stocks, the development of the genetic baseline for the species in Bristol Bay, and the protocol for its application to fisheries management, is still under development. The challenge of establishing a comprehensive baseline is much greater for Bristol Bay, considering the sheer size of the drainage basin, the difficulties in accessing and recovering samples from remote locations, and the complex

nature of the putative spawning populations in the region. Although challenging, we encourage continued development of the baseline, along with closer examination of key life-history traits that help explain differentiation among populations. These efforts not only enable more responsible fisheries management through the development of more robust, stock identification procedures leading to more effective "weak stock" management, but the sampling also provides an opportunity to test for genetic bottlenecks and generate estimates of effective population sizes that are pertinent to salmon conservation (e.g. see Habicht et al. 2004).

In the context of our larger aim to describe all extant monitoring efforts across the natural range for the genus *Oncorhynchus*, this case study has been a valuable test of our approach and helped streamline our method. We encourage broad participation in the completion of the North Pacific Salmon Monitoring Inventory and its long-term institution-
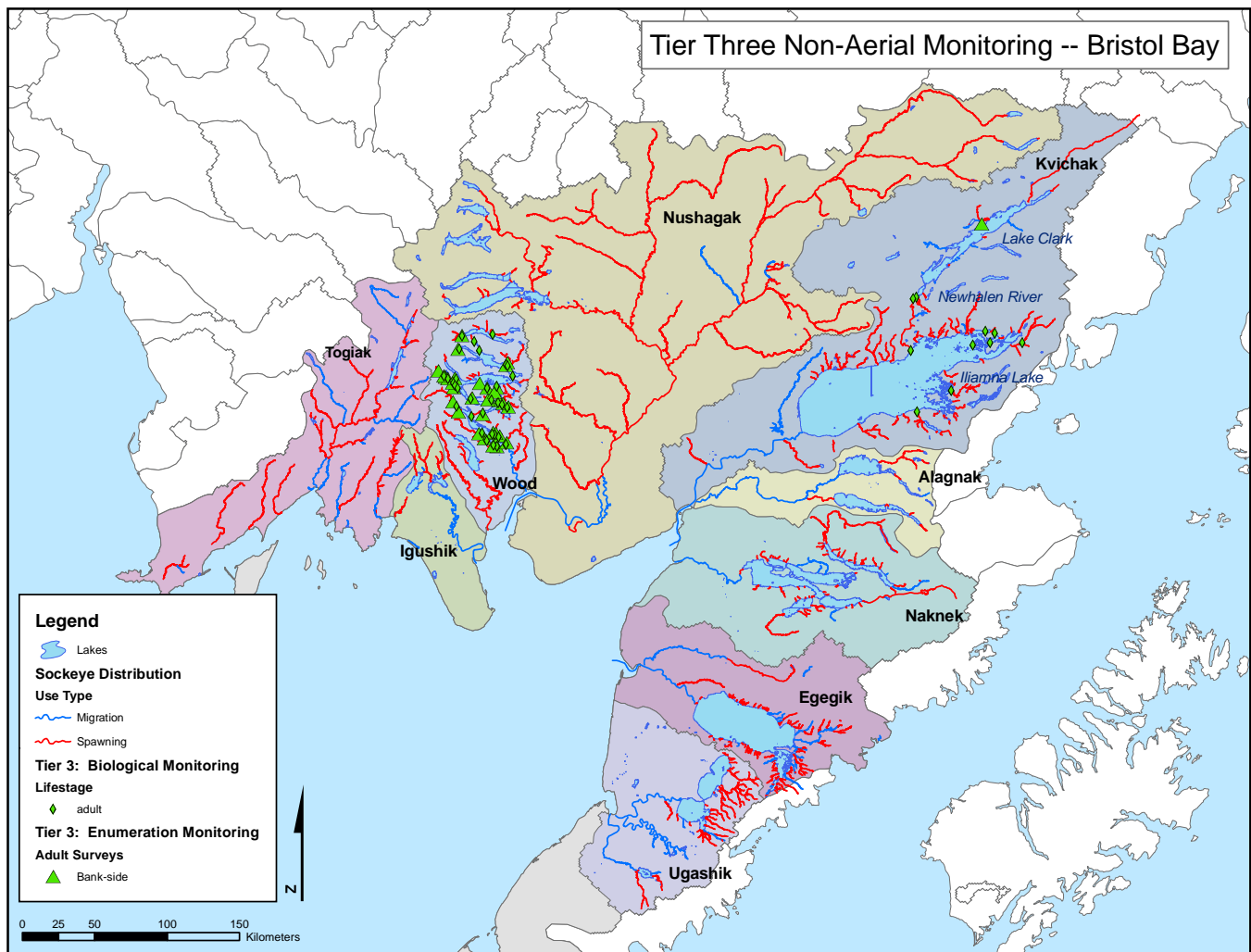
Fig. 9. Monitoring activities designated at Tier 3 within the Bristol Bay drainage, excluding aerial surveys. With the exception of some monitoring in the Kvichak River drainage, population-specific monitoring on the ground is focused exclusively in the Wood River drainage.

alization, as a fundamental building block for range-wide salmon conservation.

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Salmon as Status Indicators for North Pacific Ecosystems

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Abstract: A new system of salmon status categorization will provide useful indicators of ocean conditions and climate variability in the North Pacific Ocean. Under Canada's new Wild Salmon Policy, biological status will be assessed and categorized for a few hundred largely independent lineages of chinook, sockeye, coho, chum, and pink salmon. Changes to the status of these Conservation Units, information regarding their oceanic distribution, and biological characteristics of fish returning to fresh water to spawn will be linked to the status of marine ecosystems. Data from short-lived species like pink salmon will inform the management of longer-lived species, including fish other than salmon. Each Conservation Unit will be categorized into one of three status zones based on the abundance and distribution of spawners or proxies thereof. Intensive studies of salmon returning to selected streams will determine the relative importance of factors operating in fresh versus oceanic waters and the role of natural vs. anthropogenic factors (e.g. fishing) on Conservation Unit status. These types of information collectively should provide important clues to marine health and carrying capacity. Things should also work the other way—ecosystem data (including oceanographic) will aid in the management of salmon and other marine species.

Keywords: salmon status, marine ecosystems, North Pacific, wild salmon, Pacific salmon, wild salmon policy, marine health

INTRODUCTION

Fisheries and Oceans Canada (DFO) released a major new conservation policy for wild Pacific salmon in June 2005 (DFO 2005). The goal of the Wild Salmon Policy (WSP) is "to restore and maintain healthy and diverse salmon populations and their habitats for the benefit and enjoyment of the people of Canada in perpetuity". Wild salmon diversity will be safeguarded by protecting Conservation Units (CUs), which are groups of wild salmon living in an area sufficiently isolated from other groups that, if they are extirpated, that area is very unlikely to be recolonized naturally within an acceptable timeframe (e.g. a human life time).

This paper will briefly introduce the WSP, explain CUs, and discuss linkages between the status of wild salmon and North Pacific ecosystems.

CONSERVATION UNITS

CUs define geographically or genetically distinct groupings of salmon that generally constitute irreplaceable lineages. A taxonomic species of Pacific salmon contains more than one CU; the spatial extent occupied by a species and the genetic diversity within it are greater than for one CU (Fig. 1). Populations (reproductive groups of salmon that are relatively isolated from other such groups), demes (groups of salmon at persistent spawning sites that are likely to breed with each other), and eventually pairs of spawning salmon will normally occur further along this continuum of decreasing diversity. DFO is in the process of delineating CUs for all species of salmon within British Columbia and the Yukon Territory.

The geographic extent and number of CUs will vary among species. CUs will be identified based on biological information, including genetic variation and phenotypic traits (e.g. run timing, life-history traits, oceanic distribution), major habitat breaks representing different adaptive environments, zoogeography, and aboriginal traditional knowledge. Genetic information suggests that we should expect more CUs for sockeye salmon (*Oncorhynchus nerka*) than for other species, and that most of these will be found at the level of individual rearing lakes or rivers. Because of their varied life histories, chinook salmon (*O. tshawytscha*) will have more CUs than coho (*O. kisutch*), chum (*O. keta*), and pink salmon (*O. gorbuscha*), and the freshwater area occupied by chinook salmon CUs will therefore tend to be smaller. The freshwater environment is less important than the ocean in the definition of CUs for pink and chum salmon. These CUs will be less numerous and will coincide with salmon living in aggregates of streams that flow through major coastal regions, such as those described by Augerot et al. (2005). There will be more pink CUs than chum because
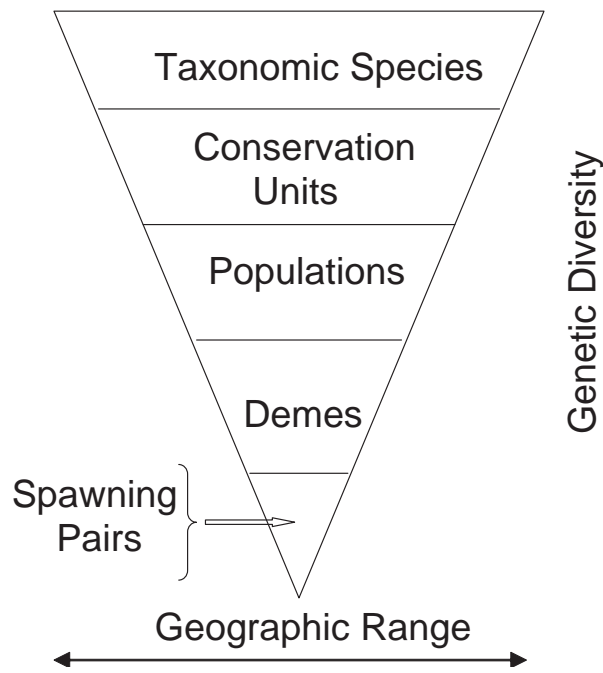
Fig. 1. Schematic illustrating the relationship between genetic diversity and geographical range for Pacific salmon (adapted from Riddell 1993).

pink salmon have two independent year lines (odd vs. even calendar years) that will constitute separate CUs.

Based on their biological status, CUs will be categorized as red, amber, or green. Status will be determined by assessing abundance (spawner escapement or proxy), distribution, diversity (genetic and life-history), and productivity (survival).

LINKING SALMON STATUS TO OCEAN STATUS

The carrying capacity of the North Pacific Ocean is an important topic to NPAFC and PICES. Salmon growth, age-at-maturity, and survival are strongly influenced by conditions experienced by salmon in the marine environment (e.g. Beamish et al. 2004; Holt and Peterman 2004) and growth can be density-dependent (e.g. Pearcy 1992). We plan to examine salmon returning to freshwater sites for evidence of changing marine conditions.

Evidence of the ocean's status can be extrapolated by monitoring the following traits in salmon when they return to fresh water:

- Size at age (i.e. marine growth)
- Age at maturity
- Return timing and changes in migratory behaviour
- Marine survival (stock recruitment)
- Oceanic distribution (based on tagging and genetic studies)
- Contaminant loads

We are in the process of designing a strategy to monitor CU status. A core programme will be established to collect the minimum agreed-upon information at all sites visited. Simulation modelling will determine the optimal annual allocation of effort needed to assess changes in CU status that may include:

- Indicator systems—comprehensive programmes usually with quantitative estimates of fishery catches plus adult and juvenile salmon abundance so that mortality can be partitioned between fresh water and marine, as well as natural and anthropogenic.
- Intensive monitoring—quantitative surveys to assess inter-annual abundance trends in CUs or CU components.

Table 1. Characteristics useful in linking salmon and ocean status[1].

| Salmon species | FW winters | Ocean winters | Relative Importance of: | | | River size | Scale of MS Corr (km) |
			Estuaries	Coastal areas	Open ocean		
Pink	0	1 (1–3)	M	M	H	Variable	500–800
Chum	0	2-4 (1–5)	H	M	H	Variable	500–800
Sockeye	1–2 (1-4)	2-3 (1–4)	M	M	H	Variable—lakes impt	500–800?
Sockeye (sea)	0	2–4	M	M	H	Variable	500–800?
Chinook (stream)	1–2	2–4 (0–6)	H	M	H	Variable	?
Chinook (ocean)	0	3–5 (2–6)	H	H	L	Med-large	?
Coho	1–2 (0–2)	1 (0–2)	M	H	L	Small-med	500–800

[1]Characteristics include: most common (ranges) freshwater (FW) and ocean ages; relative importance (L, low; M, moderate; H, high) of estuaries, near-shore coastal, and open ocean areas; and river sizes. The scale of marine survival correlations (MS Corr) for pink, chum, and sockeye are from Pyper et al. (2005); correlations are weakest for sockeye salmon. We expect similar MS correlations for coho salmon but they may be superimposed on differential survival patterns for coastal and interior CUs.

- Extensive monitoring—similar to intensive monitoring but generally less expensive and often with broad spatial coverage in order to assess relative abundance (or presence or absence), distribution, and to monitor habitat changes.

The monitoring strategy will incorporate randomisation and replication to reduce bias and increase precision, and allow for statistical inferences to be made within and among CUs.

Known animal behaviour suggesting the relevance of estuaries, coastal areas, and the open ocean (Table 1) will help link the status of CUs to various ecosystems in the North Pacific. Chinook salmon provide an interesting example of how different life-history characteristics within a species can be used to monitor changing ocean conditions. Stream-type chinook spend one to two years in freshwater environments and rely on estuaries, but pass through coastal marine areas relatively quickly en route to oceanic feeding areas. In contrast, ocean-type chinook migrate to sea in their first year, also rely on estuaries, but show prolonged use of near-shore coastal areas. Declines in the status of ocean type chinook (or coho) salmon populations may indicate poor conditions in coastal regions close to the point of natal stream entry, while similar biological responses in stream-type chinook may reflect survival problems in the open ocean. We expect pink, chum, ocean-type chinook, and sea-type sockeye will be the most helpful for identifying changing marine conditions because of their relatively brief exposure to freshwater environments. Pink salmon will probably be the most useful of these because pinks return to spawn after only one winter at sea (quick response) and do not have multiple age-classes.

NEXT STEPS

The WSP is expected to transform the management and assessment of wild salmon in Canada (Irvine and Fraser 2007). The release of the policy is only the beginning of a process. CUs need to be confirmed and a sampling approach put in place to effectively track changes in their status. Assessments will be designed to determine the role of natural vs. anthropogenic factors (e.g. fishing) as well as which stage(s) of the salmon's life history is limiting (e.g. early marine or later) and geographic distribution (coastal shore vs. open ocean). Measurements of the CUs' changing status, combined with information regarding the biological characteristics and marine distributions of fish returning from the ocean, will aid scientists in assessing changes in marine ecosystems. Things should also work the other way—ecosystem data (including oceanographic information) will aid in the management of salmon and other species. A key ingredient for the success of this policy is collaboration. We look forward to working with scientists from other agencies and nations in the development of monitoring programmes that will help link the status of salmon with their marine ecosystems. Scientists from a variety of disciplines can benefit from the data gathered from these programmes making a good plan for archiving data essential.

ACKNOWLEDGEMENTS

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Influence of Salmon Abundance and Ocean Conditions on Body Size of Pacific Salmon

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Abstract: After the North Pacific ocean climate change in 1976–77, most species of Pacific salmon (*Oncorhynchus* spp.) in North America and Asia increased in abundance and declined in body size up until the early 1990s. Several authors attributed this decline in body size of chum salmon (*O. keta*) to increasing population density of chum salmon in the ocean. In the mid-1990s, the body size of adult chum salmon increased in several streams in North America in spite of high population numbers. To determine if these increases in body size were restricted to local areas or more widespread geographically in North America, we examined data on the abundance and mean body size of salmon from commercial catches in waters from northern Alaska south to the state of Oregon among three time periods (1960–76, 1977–94, 1995–2006). Trends in body size indicate that northern and southern populations of chum, pink, and sockeye, and coho in Washington and Oregon experienced increased body size in the mid-1990s. In correlation analyses, chum, pink (*O. gorbuscha*), and sockeye salmon (*O. nerka*) body size was, in many cases, negatively related to abundance, and more negatively correlated during the 1977–94 period. For the 1960–76 period, the abundance of Pacific salmon was low, and the effect of density-dependence on the fish was the lowest. For the 1977–94 period, salmon were numerous and the effect of density on the body size of salmon was significant in many cases. For the 1995–2006 period, the abundance of salmon remained high, however, the body size of the salmon was not commonly related to population density. The 1995–2006 period appears most favorable for salmon, in that ocean resources supported salmon of large body size and large population numbers. We conclude that the carrying capacity of the North Pacific Ocean for producing Pacific salmon is not a constant value and varies with changing environmental and biological factors.

Keywords: Pacific salmon, body size, abundance, ocean regimes, density dependence, carrying capacity

INTRODUCTION

Ocean climate in the North Pacific Ocean changed dramatically after 1976 (Miller et al. 1994). Following this climate shift, Pacific salmon (*Oncorhynchus* spp.) abundance in Alaska increased to record levels by the mid 1980s (Fig. 1). However, as salmon populations were increasing in numbers, the size of individuals decreased and their age at maturity increased (Ishida et al. 1993; Helle and Hoffman 1995; Bigler et al. 1996). The decline in body size was statistically significant. For example, two North American chum salmon (*Oncorhynchus keta*) populations in Washington and one in southeast Alaska declined 46% in weight between the early 1970s and the early 1990s (Helle and Hoffman 1995). The large decline in size of chum salmon that accompanied the large increase in abundance (Fig. 2) suggested that the decline in size was density-dependent.

By the mid-1990s, these two North American chum salmon populations were showing an increase in body size (Helle and Hoffman 1998). However, commercial harvest of chum salmon in the North Pacific Ocean remained high (Fig. 2). Helle and Hoffman (1998) suggested that because body size was increasing while the population abundance remained high, another ocean climate change may have occurred.

Bigler et al. (1996) compared the size of all Pacific salmon from northern Alaska south to California from 1970 through the early 1990s and showed that all species had exhibited significant declines in size. In the present paper, we compare size changes of salmon from the early 1960s into the mid-2000s in a broad geographic area similar to the approach used by Bigler et al. (1996). Our objectives were to learn: 1) if the increase in body size of chum salmon in the mid 1990s described by Helle and Hoffman (1998) occurred throughout their range in North America, 2) if this increase

in body size occurred in all species of salmon, 3) if body size of salmon was related to abundance, and 4) if body size of salmon was related to ocean regime changes.
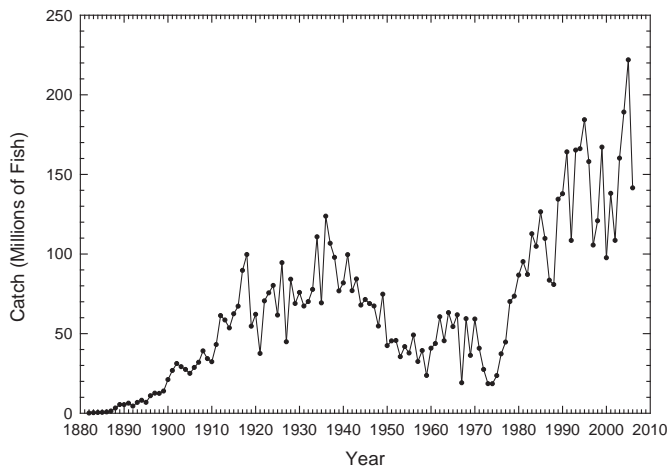

Fig. 1. Total Alaska salmon catch, 1882–2006, all species included. Data are from Alaska Department of Fish and Game.

Fig. 2. Commercial harvest of salmon in North America and in all of the Pacific Ocean (North America and Asia), 1960–2006.

MATERIALS AND METHODS

Abundance Estimates

Indices of abundances for anadromous chum, pink (*O. gorbuscha*), sockeye (*O. nerka*), coho (*O. kisutch*), and Chinook (*O. tshawytscha*) salmon were estimated as the number of salmon captured in the commercial fisheries in North American waters and the entire Pacific Ocean (North America and Asia) from 1960 to 2005. We reported abundance in millions of fish. The North Pacific Anadromous Fish Commission documents and Statistical Yearbooks were sources for harvest statistics from the commercial fisheries of Japan, Russia, Alaska, British Columbia, Washington, Oregon, and California. Commercial catch may sometimes not be a good indicator of abundance due to changes in fishing effort as a consequence of changes in monetary value, weather conditions, and social and cultural events. Data on escapement to estimate adult returns were not available for the time series used in the analysis.

Body Size Estimates

Mean body size of Pacific salmon was estimated from commercial fisheries harvest statistics from Kotzebue in northern Alaska to the state of Oregon for 1960 to 2006. Mean body weight (kg) was calculated as the total biomass of salmon captured (kg) during year t divided by the numbers of salmon captured (N) during year t. Mean body weight was calculated for chum, pink, sockeye, coho, and Chinook salmon.

Regions included Kotzebue, Norton Sound, Kuskokwim, Yukon during the summer salmon run, Yukon during the fall run, Bristol Bay, central Alaska, southeast Alaska, northern British Columbia, Washington, and Oregon (Fig. 3). Mean size of central Alaska salmon was calculated as the average of the average size of salmon from the Alaska Peninsula, Chignik, Kodiak, Cook Inlet, and Prince William Sound areas (Fig. 3). Chinook size was not presented for Oregon, Washington, northern British Columbia, and southeast Alaska due to size restrictions in the troll fisheries.

Biomass and numbers from salmon harvest statistics were available from several sources. For Alaska, the Alaska Department of Fish and Game (ADFG) provided biomass and numbers for pink, chum, sockeye, coho, and Chinook captured from commercial fisheries management regions in Alaska from 1960 to 2006 (Doug Eggers, Alaska Department of Fish and Game, Commercial Fisheries Division, P.O. Box 25526, Juneau, AK 99802-5526). The 1960–76 data originated from International North Pacific Fisheries Commission Bulletin 79 and the 1977–2006 data from ADFG fish tickets. For northern British Columbia, the Department of Fisheries and Oceans' Division of Data and Statistics webpage was the source of biomass and numbers for chum, pink, sockeye, and coho salmon captured in the Area 3 management region in
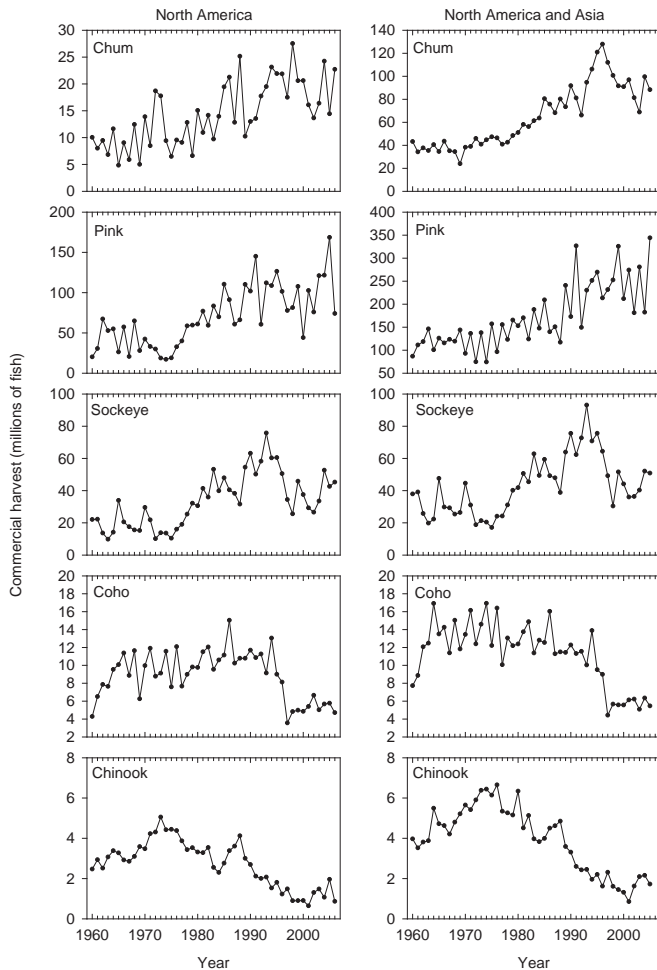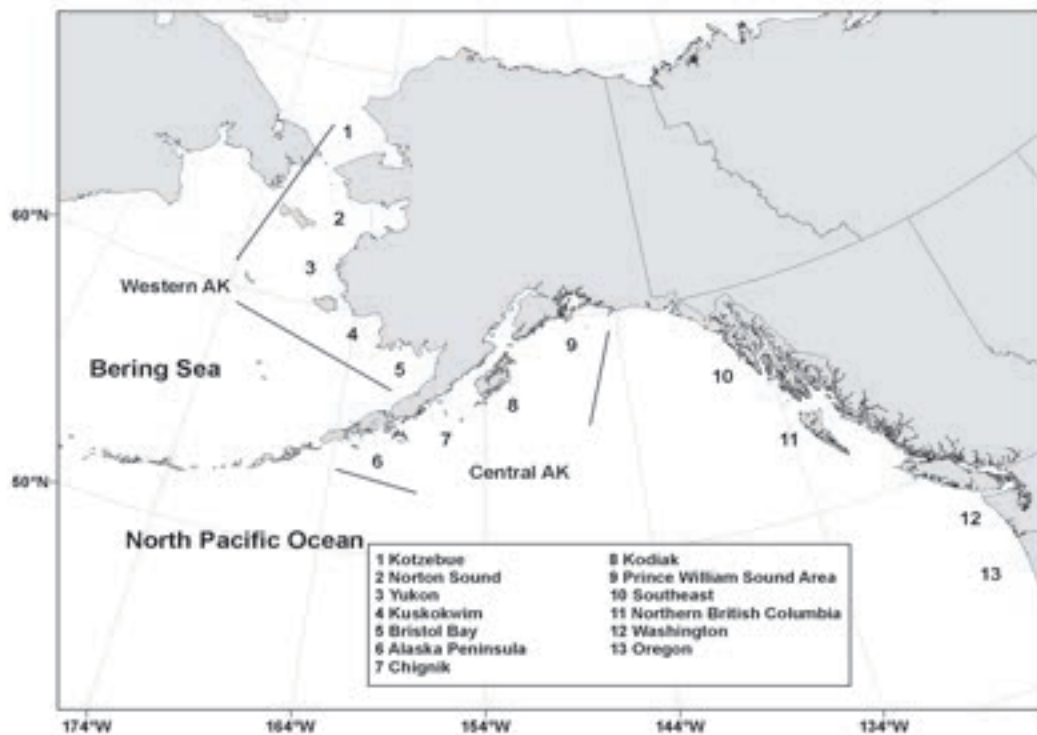
Fig. 3. Locations of salmon populations examined for changes in body size over time.

waters off northern British Columbia, Canada from 1969 to 2006 (DFO 2006). For Washington, the Washington Department of Fish and Wildlife provided biomass and numbers for chum, pink, and sockeye salmon harvested from the Puget Sound commercial fishery for years from 1980 to 2004 (Lee Hoines, Washington Department of Fish and Wildlife, Natural Resources Building, 1111 Washington St. SE, Olympia, WA 98501; Hoineljh@dfw.wa.gov). For Oregon, the Oregon Department of Fish and Wildlife provided biomass and numbers for coho salmon harvested from the commercial ocean troll salmon fishery off the Oregon coast from 1979 to 2004 (Eric Schindler, Oregon Department of Fish and Wildlife, Marine Resources Program, 2040 SE Marine Science Drive, Newport, OR 97365).

Trends in Body Size and Abundance of Salmon

Line plots were used to show the inter-annual variation in mean body size and salmon abundance over time. To show the low-frequency trends over time we fitted a locally weighted smoothed regression line to annual values of mean body size (Cleveland and Devlin 1988). Smoothing options were specified as a 0.3 span value and a one degree linear fitting.

Relation between Body Size and Abundance of Salmon

The relationships between mean body size of salmon populations and the abundance of Pacific salmon were de-

scribed using the Pearson product moment correlation coefficient. The coefficient measures the tendency of the variables to increase or decrease together. The coefficient is calculated by dividing the covariance between the two variables by the product of their standard deviations. Analyses were conducted using SigmaStat statistical software (1997). Coefficients were considered statistically significant at the $P < 0.05$ level (*) and more significant at $P < 0.01$ (**).

Comparisons were made between salmon body size and salmon abundance indices during three time periods. The time periods were: pre- ocean regime change, 1960–76; ocean regime change 1977–94; and post ocean regime change 1995–2005. Designations for time periods were based on the 1976–77 ocean regime shift (Hare and Francis 1995), and the 1995 increase in body size of chum salmon at Fish Creek, Hyder, Alaska (Helle and Hoffman 1998). Comparisons were made between salmon size and catch in North America and in the North Pacific Ocean (North America and Asia) because populations from North America and Asia are known to intermingle in the North Pacific Ocean (Myers et al. 1996).

RESULTS

Abundance of Salmon

Catches of chum salmon in both Asia and North America have generally been increasing since the ocean climate change of 1976–77 (Fig. 2). Asian chum salmon reached peak num-

bers in 1996, while chum salmon in North America reached peak numbers in 1998. The abundance of chum salmon has remained at relatively high levels from the mid 1990s to the mid 2000s. Asian and North American pink salmon have also been generally increasing in abundance since the mid 1970s.

Sockeye salmon catches also increased after the mid 1970s and peaked in abundance in both Asia and North America in 1993 (Fig. 2). However, sockeye salmon abundance declined from 1993 to 1998, and remained relatively constant from 1998 to 2005.

Coho salmon, unlike chum, pink, and sockeye, do not show an increase in abundance following the mid 1970s (Fig. 2). Coho salmon abundance increased during the early 1960s and remained at relatively high levels until a large drop in 1997. Coho salmon have remained at lower levels to the present time.

Chinook salmon show a trend in abundance opposite to that of chum, pink, and sockeye salmon (Fig. 2). The total North Pacific and North American catch of Chinook salmon increased from 1960 to the mid 1970s, and then declined from the mid 1970s to the mid 2000s (Fig. 2).

Body Size of Salmon

Chum salmon

Except for Yukon River fall chum salmon, populations in western Alaska (areas 1–5 on Fig. 3) showed a decline in body size after the mid 1970s with a reversal in this trend toward larger body size after the mid 1990s (Fig. 4). Chum

salmon from central Alaska south to the state of Washington (areas 6–13 on Fig. 3) show remarkable similarity in declining size, reaching a low point in 1993. They then show a general increasing trend in body size until another significant drop starting in 2003 (Fig. 5).

Pink Salmon

Pink salmon populations from Bristol Bay in western Alaska south to Washington show a decline in body size be-

Fig. 5. Mean body weight of chum salmon from central Alaska, southeast Alaska, northern British Columbia (Canada), and Washington, 1960–2006.
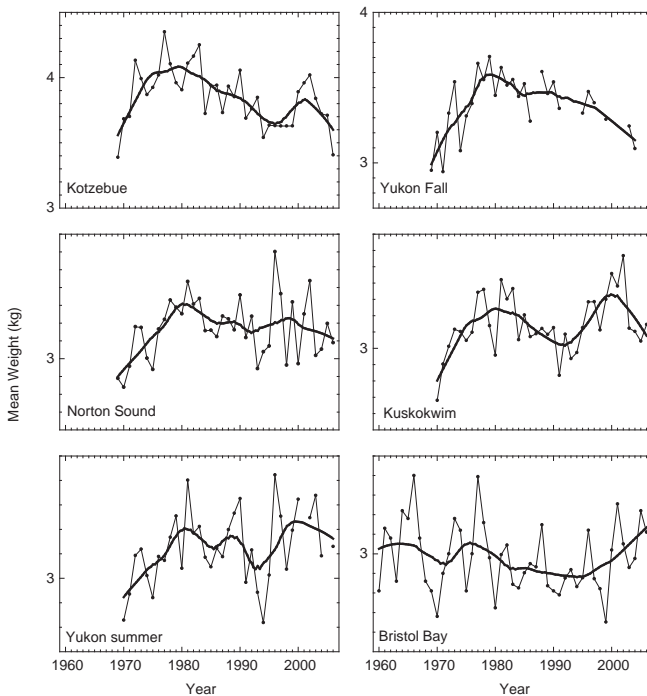

Fig. 4. Mean body weight of chum salmon from Kotzebue, Norton Sound, Yukon River summer, and Yukon River fall, 1969–2006.

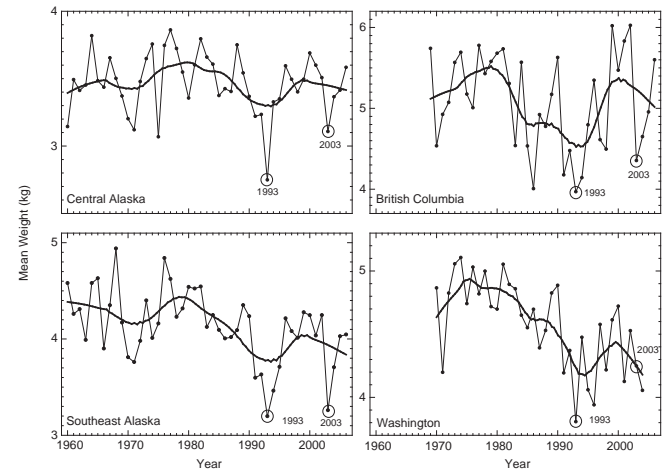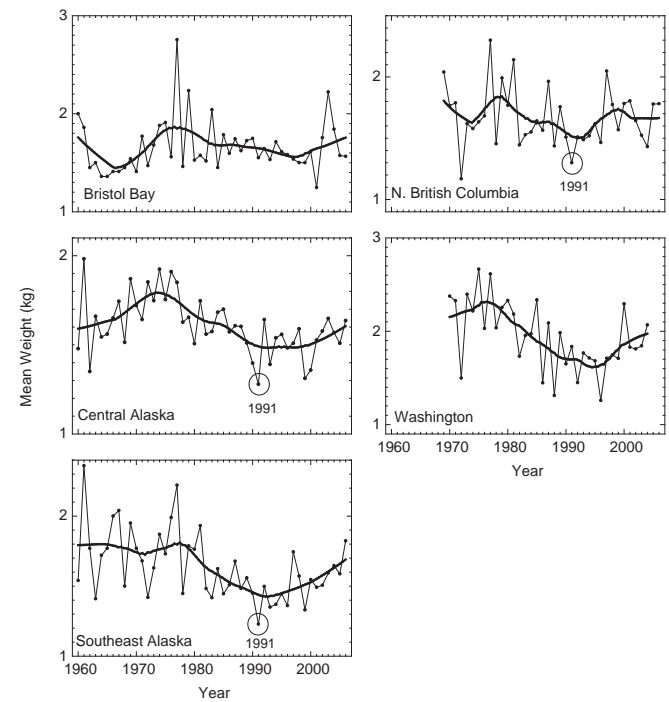**Fig. 6.** Mean body weight of pink salmon from Bristol Bay, central Alaska, southeast Alaska, British Columbia (Canada), and Washington, 1960–2006.

ginning in the mid 1970s and continuing through the early 1990s (Fig. 6). A low point in the decline in pink salmon size occurred in 1991, except for populations in the most northerly and most southerly areas (Fig. 6). From the early 1990s

to the present time, the size of pink salmon has generally increased. However, pink salmon in the 2000s are not as large as they were in the mid 1970s (Fig. 6).

Sockeye Salmon

Sockeye salmon populations from Bristol Bay south to Washington show a decline in body size after the mid 1970s to the mid 1990s (Fig. 7). After the mid 1990s, the body size of sockeye salmon increased slightly; however, by the mid 2000s size again declined.

Coho Salmon

Size of Kuskokwim River coho salmon is highly variable (Fig. 8). Body size of coho salmon from central and southeast Alaska has been declining since the late 1980s. Populations from northern British Columbia, Washington, and Oregon declined in size from the early 1970s through the early 1990s (Fig. 8). After the early 1990s these southern coho salmon populations increased in body size.

Chinook Salmon

Chinook salmon from the Yukon River in the north through central Alaska all show a continuous decline in body size from the mid 1970s to the present time (Fig. 9).

Relation between Body Size and Abundance of Salmon

Correlations between body size and abundance among populations of chum, pink, and sockeye salmon were negative (Tables 1 and 2). Correlations between coho and Chinook salmon were mixed, some negative, some positive. Chum, pink, and sockeye salmon showed a greater number of significant correlations between size and abundance during the period following the climate shift in the North Pacific Ocean in 1977–94 (Tables 1 and 2), than in 1960–76 and 1977–2005. Correlations with chum salmon were also

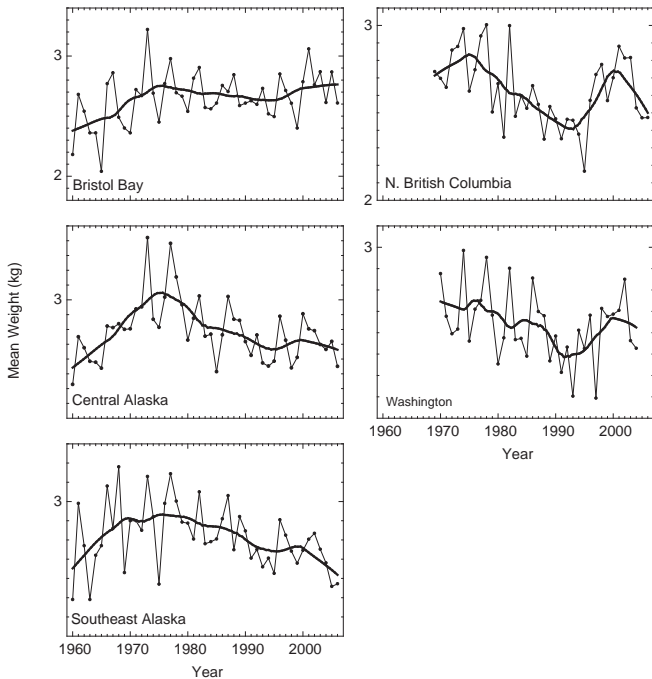**Fig. 7.** Mean body weight of sockeye salmon from Bristol Bay, central Alaska, southeast Alaska, British Columbia (Canada), and Washington, 1960–2006.
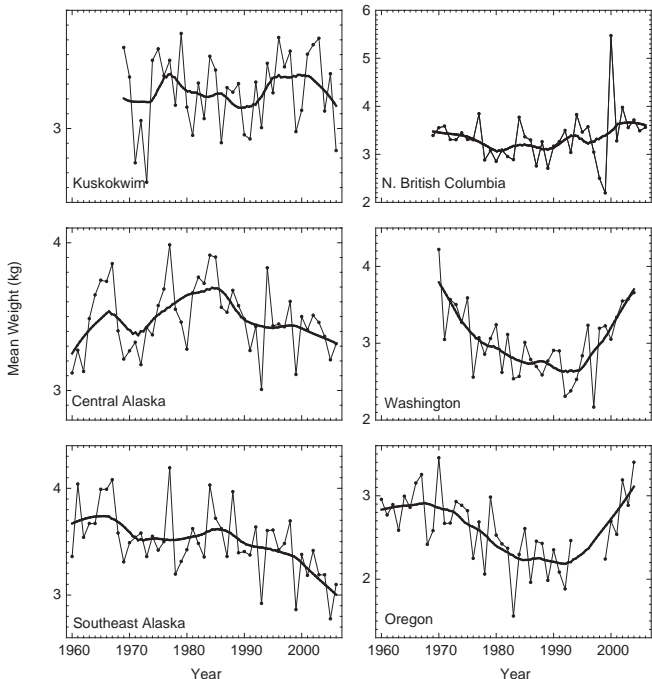

Fig. 8. Mean body weight of coho salmon from Kuskokwim, central Alaska, southeast Alaska, and British Columbia (Canada), Washington, and Oregon, 1960–2006.
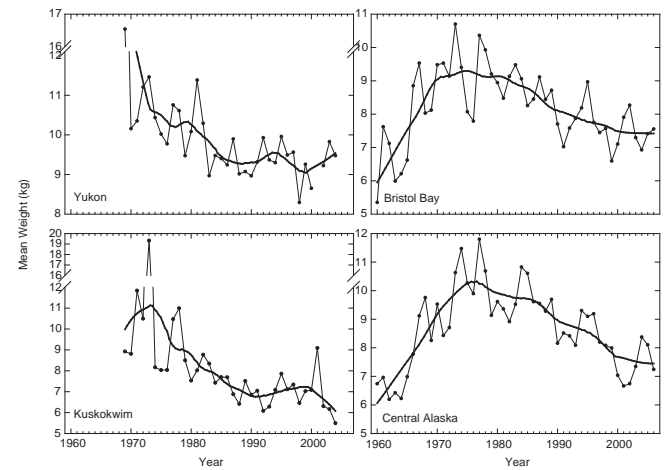

Fig. 9. Mean body weight of Chinook salmon caught from Yukon, Kuskokwim, Bristol Bay, and central Alaska, 1960–2006.

Table 1. Pearson correlation coefficients relating mean body size of Pacific salmon to the total commercial catch of salmon in North America. Gray columns indicate no significant correlation.

BODY SIZE	AREA	1960–1976 CATCH					1977–1994 CATCH					1995–2005 CATCH				
		Chum	Pink	Sockeye	Coho	Chinook	Chum	Pink	Sockeye	Coho	Chinook	Chum	Pink	Sockeye	Coho	Chinook
CHUM	Kotzebue	0.585	-0.305	-0.477	0.327	0.797*	-0.475*	-0.530*	-0.431	-0.362	0.548*	-0.237	-0.067	-0.539	-0.183	-0.579
	Norton Sound	0.544	-0.309	-0.56	0.253	0.697*	-0.472*	-0.554*	-0.444	-0.130	0.482*	-0.190	0.055	0.038	0.207	-0.052
	Yukon R. Summer	0.358	-0.446	-0.678	0.052	0.691	-0.440	-0.339	-0.217	-0.004	0.448	-0.168	-0.058	-0.200	-0.118	-0.38
	Yukon R. Fall	0.536	-0.230	-0.076	-0.005	0.780*	-0.393	-0.598*	-0.345	-0.615*	0.481	0.136	-0.182	-0.086	0.275	0.114
	Kuskokwim	-0.223	-0.805*	-0.324	-0.020	0.850*	-0.337	-0.605**	-0.434	-0.224	0.495*	0.192	-0.356	-0.408	-0.150	-0.581
	Bristol Bay	0.018	0.081	0.028	0.303	-0.073	-0.143	-0.622**	-0.615**	-0.362	0.658**	-0.180	-0.097	-0.188	0.218	-0.418
	Central AK	0.084	0.056	-0.246	0.364	0.091	-0.264	-0.625**	-0.765**	-0.127	0.705**	0.347	-0.309	-0.096	-0.026	-0.469
	Southeast AK	-0.094	0.081	0.024	0.001	-0.150	-0.490*	-0.602**	-0.718**	-0.194	0.745**	0.262	-0.254	-0.166	-0.093	-0.327
	N British Columbia	-0.401	-0.779*	-0.638	-0.354	0.093	-0.589**	-0.593**	-0.584**	-0.408	0.586**	0.090	0.158	-0.128	0.069	-0.620*
	Washington	0.110	-0.322	-0.294	-0.101	0.401	-0.394	-0.474*	-0.528*	0.048	0.514*	0.009	-0.235	-0.406	-0.642*	-0.139
PINK	Bristol Bay	-0.078	-0.583*	-0.131	-0.357	0.240	-0.500*	-0.391	-0.303	-0.444	0.286	-0.136	0.007	0.069	-0.018	0.327
	Central AK	-0.059	-0.561*	-0.151	0.071	0.091	-0.128	-0.729**	-0.596**	-0.207	0.512*	-0.370	-0.104	-0.213	0.130	0.269
	Southeast AK	-0.432	-0.174	0.295	0.019	-0.113	-0.434	-0.692**	-0.620**	-0.379	0.594**	-0.378	-0.384	-0.331	-0.591	0.346
	N British Columbia	-0.665*	0.237	0.467	-0.154	-0.454	-0.463*	-0.534*	-0.449	-0.347	0.483*	-0.265	-0.259	-0.507	-0.531	0.031
	WA	-0.589	-0.208	0.266	-0.140	0.187	-0.625**	-0.282	-0.440	-0.604**	0.315	0.088	-0.211	-0.205	-0.481	-0.223
SOCKEYE	Bristol Bay	0.376	-0.176	-0.374	0.327	0.506*	-0.041	-0.488*	-0.486*	-0.143	0.637**	-0.464	0.027	-0.446	-0.107	-0.378
	Central AK	0.473	-0.251	-0.283	0.414	0.783**	-0.524*	-0.794**	-0.751**	-0.452	0.773**	-0.001	-0.192	-0.142	0.019	-0.117
	Southeast AK	0.423	0.164	0.139	0.672**	0.295	-0.500*	-0.675**	-0.698**	-0.236	0.759**	0.234	-0.589	-0.410	-0.088	-0.436
	N British Columbia	0.343	-0.476	-0.378	0.177	0.247	-0.348	-0.563*	-0.594**	-0.258	0.545*	-0.114	-0.427	-0.904**	-0.686*	-0.680*
	Washington	-0.163	0.170	0.470	0.568	-0.472	-0.065	-0.618**	-0.651**	0.172	0.648**	0.277	-0.001	-0.331	0.189	-0.676*
COHO	Kuskokwim	-0.691	0.014	-0.078	-0.284	-0.398	-0.138	-0.390	-0.329	-0.260	0.206	-0.332	-0.197	-0.510	0.084	-0.072
	Central AK	-0.390	-0.052	0.113	0.455	0.095	0.084	-0.333	-0.407	0.094	0.280	0.351	-0.756**	-0.417	0.041	-0.117
	Southeast AK	-0.343	0.105	0.366	0.172	-0.464	0.220	-0.341	-0.460*	0.074	0.292	0.525	-0.730**	-0.128	0.213	0.094
	British Columbia	-0.032	0.523	0.811*	0.383	-0.552	0.325	0.026	-0.012	0.144	-0.265	0.150	-0.265	0.029	0.094	-0.081
	Washington	0.342	0.153	0.33	-0.629	-0.446	-0.453*	-0.197	-0.582**	-0.133	0.539	-0.003	0.228	-0.077	0.139	-0.463
	Oregon	0.077	-0.075	0.395	-0.115	-0.200	-0.136	-0.267	-0.356	-0.277	0.456	-0.193	-0.617	0.095	0.654	0.633
CHINOOK	Yukon R	-0.391	-0.059	-0.155	-0.698	-0.597	-0.280	-0.552*	-0.521*	-0.274	0.393	-0.62	0.664*	0.571	0.423	0.683*
	Kuskokwim	0.547	-0.28	-0.078	-0.039	0.468	-0.550*	-0.496*	-0.670**	-0.396	0.537*	-0.010	0.213	-0.031	0.190	-0.362
	Bristol Bay	0.353	-0.284	-0.056	0.467	0.634**	-0.429	-0.759**	-0.717**	-0.492*	0.691**	-0.084	0.030	0.093	0.661*	0.227
	Central AK	0.191	-0.443	-0.195	0.458	0.794**	-0.202	-0.445	-0.671**	-0.339	0.487*	0.241	0.102	0.763**	0.560	0.673*

more frequently significant when body size was compared to abundance of the total Pacific Ocean catch (Table 2) rather than the North American catch.

DISCUSSION

Declines in body size of North American and Asian populations of Pacific salmon occurred from the mid 1970s to the mid 1990s (Ishida et al. 1993; Helle and Hoffman 1995, 1998; and Bigler et al. 1996). These authors suggested that the declines in body size may have been caused by the increase in abundance of salmon and the resulting density-dependent competition for resources. The increased salmon abundance in the North Pacific Ocean from the mid 1970s through the mid 1900s has been attributed to enhanced food production resulting from coastal ocean warming in the eastern North Pacific Ocean following a climate change in 1976–77 (McLain 1984; Beamish and Bouillon 1993; Miller et al. 1994; and Hare and Francis 1995).

Helle and Hoffman (1995) described a steep decline in body size for two North American chum salmon populations between the early 1970s and the early 1990s, and suggested that the decline may have been caused by increasing population density during this time. In the mid 1990s, however, these two populations showed an increase in body size even though population abundance remained high (Helle and

Hoffman 1998). These authors suggested that increasing body size at high population abundance levels may have signaled a change in ocean climate in the North Pacific Ocean. The changes in the body size in the two populations described by Helle and Hoffman (1995 and 1998) were highly significant. Sample sizes were generally large within years over the 24-year sampling period. In addition, their data on chum salmon size was age-specific so changes in size were not obscured by combining multiple age groups.

The concordance of all the chum salmon populations examined in the North Pacific Ocean (south of the Bering Sea) to increase in body size after attaining a common smaller size in 1993 (Fig. 5) would suggest that some common event was responsible for the small size in 1993 and the rebound in size thereafter. In general, chum salmon in the Bering Sea show a decline in size after the mid 1970s and an increase in size after the mid 1990s (Fig. 4); however, the time of these size changes is different from those populations in the North Pacific Ocean south of the Bering Sea.

The body size of pink salmon in populations from Alaska tend to show a decline in size after the mid 1970s, reach a low point about 1991, and rebound in size thereafter (Fig. 6). This 1991 low point in size for pink salmon occurred two years before the 1993 low point in size body size of chum salmon. Pink salmon mature as 2-year-olds, and chum salmon mature mostly as 3-, 4-, and 5-year-olds; however, 4

Table 2. Pearson correlation coefficients relating mean body size of Pacific salmon to the total commercial catch of salmon in North America and Asia (total Pacific Ocean catch). Gray columns indicate no significant correlation.

BODY SIZE	AREA	1960–1976 CATCH					1977–1994 CATCH					1995–2005 CATCH				
		Chum	Pink	Sockeye	Coho	Chinook	Chum	Pink	Sockeye	Coho	Chinook	Chum	Pink	Sockeye	Coho	Chinook
CHUM	Kotzebue	0.898*	-0.394	-0.529	0.222	0.769*	-0.602**	-0.453	-0.446	-0.021	0.581**	-0.634*	-0.289	-0.632	-0.272	-0.681*
	Norton Sound	0.522	-0.296	-0.593	0.270	0.649	-0.605**	-0.519*	-0.455	0.172	0.538*	0.347	-0.128	0.188	0.001	0.001
	Yukon R. Summer	0.437	-0.188	-0.681	0.636	0.208	-0.404	-0.421	-0.241	0.128	0.384	-0.156	-0.152	-0.101	-0.351	-0.351
	Yukon R. Fall	0.584	-0.084	-0.336	-0.045	0.716*	-0.444	-0.315	-0.373	-0.430	0.355	0.598	0.108	0.484	0.328	0.328
	Kuskokwim	0.684	0.096	-0.914**	0.267	0.784*	-0.586*	-0.529*	-0.467*	0.156	0.466*	-0.133	-0.456	-0.325	-0.538	-0.538
	Bristol Bay	0.176	-0.123	-0.050	-0.052	-0.052	-0.471*	-0.468*	-0.633**	-0.107	-0.205	0.037	-0.386	-0.159	0.213	-0.479
	Central AK	0.027	-0.321	-0.295	0.463	0.208	-0.630**	-0.540*	-0.805**	0.236	0.633**	0.340	-0.272	0.077	0.110	-0.357
	Southeast AK	-0.058	-0.058	0.037	0.025	-0.041	-0.726**	-0.536*	-0.727**	0.203	0.816**	0.261	-0.122	0.009	0.027	-0.209
	N British Columbia	-0.304	0.210	-0.625	0.002	0.136	-0.672**	-0.478*	-0.583**	-0.022	0.650**	-0.116	-0.017	-0.103	0.090	-0.611*
	Washington	0.381	-0.443	-0.260	0.080	0.816*	-0.565*	-0.477*	-0.569**	0.436	0.574**	-0.441	0.056	-0.336	-0.618*	-0.053
PINK	Bristol Bay	0.315	-0.023	-0.087	-0.309	0.096	-0.337	-0.028	-0.326	-0.411	0.215	-0.459	-0.189	-0.182	-0.185	0.161
	Central AK	0.060	-0.380	-0.169	0.043	0.429	-0.579**	-0.577**	-0.608**	0.085	0.459	-0.132	-0.206	-0.293	0.025	0.171
	Southeast AK	-0.207	-0.007	0.316	-0.123	-0.139	-0.651**	-0.417	-0.614**	-0.128	0.599**	-0.212	-0.227	-0.355	-0.623*	0.366
	N British Columbia	-0.745*	0.560	0.466	0.005	-0.454	-0.503*	-0.213	-0.451	-0.186	0.460*	0.028	0.148	-0.192	-0.407	0.208
	WA	-0.286	0.731	0.197	0.039	-0.038	-0.562*	0.053	-0.429	-0.276	0.470*	-0.567	-0.211	-0.408	-0.548	-0.283
SOCKEYE	Bristol Bay	0.246	0.032	-0.427	0.264	0.337	-0.354	-0.415	-0.485*	0.022	0.426	-0.249	-0.048	-0.349	-0.104	-0.413
	Central AK	0.215	0.099	-0.389	0.403	0.639**	-0.766**	-0.557**	-0.766**	-0.099	0.635**	-0.001	-0.387	-0.058	0.049	-0.388
	Southeast AK	0.089	-0.196	0.044	0.443	0.263	-0.674**	-0.511*	-0.706**	0.113	0.696**	0.195	-0.598	-0.274	-0.011	-0.351
	N British Columbia	0.180	-0.602	-0.384	0.331	0.478	-0.647**	-0.507*	-0.589**	0.216	0.589**	-0.537	-0.218	-0.878**	-0.663	-0.625*
	Washington	-0.273	-0.607	0.443	0.548	0.078	-0.465*	-0.662**	-0.680**	0.541*	0.521*	-0.335	-0.084	-0.413	0.156	-0.751**
COHO	Kuskokwim	-0.110	-0.106	-0.013	-0.265	-0.006	-0.258	-0.186	-0.335	-0.129	0.146	-0.040	-0.148	-0.354	0.085	-0.080
	Central AK	0.126	0.247	-0.028	0.376	0.129	-0.196	-0.280	-0.452	0.271	0.193	0.112	-0.644*	-0.337	0.071	-0.102
	Southeast AK	-0.153	-0.011	0.373	-0.114	-0.499*	-0.167	-0.305	-0.471*	0.076	0.186	0.473	-0.602*	0.018	0.288	0.171
	British Columbia	-0.323	-0.077	0.768*	-0.564	-0.564	0.204	0.075	-0.019	0.043	-0.337	-0.149	-0.491	-0.036	0.048	-0.185
	Washington	-0.384	-0.015	0.417	-0.459	-0.459	-0.453	-0.111	-0.564**	0.176	0.673**	-0.536	-0.124	-0.421	-0.001	-0.657*
	Oregon	0.060	-0.154	0.398	-0.157	-0.157	-0.159	-0.149	-0.323	-0.127	0.414	-0.047	-0.851*	-0.386	0.485	-0.130
CHINOOK	Yukon R	-0.879**	0.335	-0.037	-0.584	-0.513	-0.643**	-0.357	-0.498*	0.129	0.452	0.159	0.149	0.521	0.333	0.517
	Kuskokwim	-0.051	0.292	-0.114	0.076	0.104	-0.726**	-0.306	-0.695**	0.136	0.583**	0.336	0.251	0.264	0.327	-0.232
	Bristol Bay	0.118	0.006	-0.167	0.346	0.524*	-0.749**	-0.558*	-0.739**	-0.009	0.717**	0.363	-0.151	0.258	0.654*	0.197
	Central AK	0.330	-0.081	-0.324	0.414	0.758**	-0.529*	-0.294	-0.691**	0.004	0.494*	0.780**	0.065	0.809**	0.604*	0.698*

years is a common age at maturity for chum salmon throughout North America (Salo 1991). Four-year-old chum salmon returning in 1993 and pink salmon returning in 1991 would be from the same brood year (1989). A relation between the size at maturity of pink and chum salmon from the same brood year is not likely because Helle (1979) showed that chum salmon of different ages show a similarity in size at maturity based on return year and not brood year. Therefore, growth in the last year in the ocean is very important in determining final size at maturity. The commonality in the North Pacific Ocean for most pink salmon to reach a low point in size in 1991 may be associated with the large numbers of maturing pink salmon in the North Pacific Ocean in 1991 (Fig. 2). The reason for chum salmon to reach a low point in size in 1993 may be related to abundance (Fig. 2), but the association with large population abundance is not as clear as it is for pink salmon.

Population density, as mentioned previously, was strongly suspected of being a major influence in the long-term decline in size in Pacific salmon in the mid 1970s to the early 1990s. The influence of intra-species population density and/or inter-species population density being a factor in the increase in size at maturity of chum salmon after the mid 1990s is unlikely, because population numbers generally remained high after the mid 1990s (Figs. 1 and 2).

North American and Asian populations of salmon, espe-cially chum salmon, are known to intermingle in the North Pacific Ocean (Salo 1991; Myers et al. 1996; Ruggerone et al. 2003; Urawa et al. 2005; Habicht et al. 2005). Assuming that size at maturity is strongly influenced by factors during the final year in the ocean, then many populations of Asian and North American salmon should exhibit similar changes in size of returning adults. An exception to this argument may be in populations of chum and Chinook salmon entering rivers that discharge into the Bering Sea. For example, many maturing chum and Chinook salmon enter the Yukon River in June and early July so the last summer growing season is shortened. The penultimate year may be important in determining final size at maturity for these northern populations. In all species, except coho salmon, significant correlations between body size and abundance of salmon were far more common during 1977–94 than during 1960–76 or 1995–2005 (Tables 1 and 2). Following the 1976–77 ocean climate change, population abundance of chum, pink and sockeye salmon increased greatly during 1977–94 (Fig. 2). During the next time period, 1995–2005, abundance of chum and pink salmon generally remained high, while sockeye salmon abundance declined. Coho salmon did not show a clear trend in relationships between size and abundance among the three time periods.

During 1977–94, chum salmon body size was negative-ly related in many cases to the total Pacific catch of chum,

pink, and sockeye salmon; positively related to the total Pacific catch of many Chinook salmon populations; and not related to the total Pacific catch of coho salmon (Table 2). The body size of chum salmon was negatively related to the abundance of pink salmon in North America, with the exception of summer chum salmon from the Yukon River. The total Pacific catch of pink salmon was negatively related to the body size of all chum populations, except for summer and fall Yukon River chum salmon and Kotzebue chum salmon (Tables 1 and 2). Body size of chum salmon populations from Bristol Bay south to Washington were negatively related to abundance of sockeye salmon in both North America and the total Pacific catch (Tables 1 and 2). Kuskokwim River chum salmon were also negatively related to the total Pacific catch of sockeye salmon (Table 2). During 1960–76 and 1995–2005, there were only sporadic negative and positive correlations (Table 1). These results suggest that chum, pink, and sockeye salmon were competing for resources and that competition intensified for the 18 years following the 1976–77 ocean regime change.

Chum salmon body size was more negatively correlated with total Pacific catch of chum salmon than with the North American catch of chum salmon. For 1977–94, when comparing chum salmon body size to the total Pacific Ocean catch of chum salmon, only Yukon River chum salmon did not show a significant negative relation (Table 2). However, in 6 out of 10 populations during this time, chum salmon size did not show significant relationships to the abundance of North American populations (Table 1). Clearly, there is competition for resources among most North American and Asian chum salmon in the North Pacific Ocean.

Pink salmon body size in comparison with abundance during the same time periods and locations of catches show a pattern similar to that described for chum salmon in that there are more significant relations during 1977–94 than during the earlier and later time periods (Tables 1 and 2). Moreover, as with chum salmon, most of the significant relationships with pink salmon size are negative with chum and sockeye abundance, positive with Chinook salmon abundance, and with few significant negative correlations with coho salmon abundance. During 1960–77, the body size of northern British Columbia pink salmon was negatively related to the abundance of chum salmon in both the North American catch and the total Pacific catch (Tables 1 and 2). During 1960–77, Bristol Bay and central Alaska pink salmon size related negatively to the abundance of pink salmon in North American catches (Table 1), but not negatively to the total Pacific Ocean catch of pink salmon (Table 2). During 1995–2005, there was only one significant correlation between pink salmon body size and abundance in both the North American catches and the total Pacific Ocean catches. Further, with only one minor exception (Washington pink salmon) pink salmon body size was more significantly correlated with the North American catch than with the total Pacific Ocean catch. This result is expected because the ocean

distributions of Asian and North American pink salmon, in most cases, show only minor overlap (Myers et al. 1996).

Significant relationships between sockeye salmon size and abundance are far more common during 1977–94, than the earlier and later periods in both the comparisons with the total Pacific Ocean catch and the North American catch (Tables 1 and 2). Similar to chum and pink salmon body size, sockeye size was negatively correlated with chum, pink, and sockeye abundance, and positively correlated with Chinook salmon abundance. Of the five sockeye populations in North America, only Bristol Bay sockeye were not significantly correlated with chum salmon abundance in the Pacific Ocean and North America (Tables 1 and 2).

Coho salmon show fewer significant relationships between size and abundance than the other species (Tables 1 and 2). Coho salmon are generally not as abundant as chum, pink and sockeye salmon and may not be competing for resources with these species (Fig. 2). Numbers of coho salmon declined precipitously in 1997 and have remained at lower levels to the present time (Fig. 2). Body size of coho increased in the 2000s in northern British Columbia, Washington, and Oregon; however, body size of coho salmon in southeast Alaska and central Alaska appears to be declining. Response of body size to abundance in coho salmon appears to be more related to local conditions than to the abundance of other salmon species because of their brief (one winter and two summers) time at sea. Time in the ocean of coho salmon is similar to that of pink salmon.

Chinook salmon are generally in lower abundance than chum, pink, sockeye, and coho salmon (Fig. 2). However, Chinook salmon show more significant correlations than coho salmon with abundance of the other species of salmon. Chinook salmon spend more years at sea than coho salmon and that may account for the differences. In addition, the declines in Chinook salmon catches since the early 1970s may account for the positive correlations between size of chum, pink, and sockeye salmon and Chinook salmon abundance.

CONCLUSIONS

In the present paper, we compare salmon body size over a broad geographic area, from the northern Bering Sea south to the state of Oregon. The data we have used comes from commercial catch records and age composition within species was generally not available. Nevertheless, due to the large sample sizes, we observed spatial and temporal trends in body size over time. We are also aware of the potential caveats of using catch data as a surrogate for abundance; but, because of the multiple years involved, we think that the trends were not obscured.

After a significant decline in body size associated with an increase in abundance of North American chum salmon from about 1980 to the early 1990s, most populations showed an increase in body size during the late 1990s. However, abundance did decline after the peak numbers of the mid to

late 1990s but still remained at high levels. Pink salmon abundance showed increases similar to those of chum salmon, but sockeye salmon declined after the mid 1990s. Chum salmon body size is, in many cases, related negatively to the abundance of pink and sockeye salmon. Body size of pink and sockeye salmon also tended to follow the same pattern as chum salmon but there were some regional differences. Body size of coho salmon was highly variable. Central and southeastern Alaska coho populations declined in body size after the early 1980s and are still in decline into the mid 2000s. Northern British Columbia, Washington, and Oregon populations of coho salmon declined in body size from the early 1970s to the early 1990s, and then increased through the early 2000s. Body size and abundance of Chinook salmon from the Yukon River south to central Alaska have been declining in size since the early 1970s. We did not look at size of Chinook salmon from southeastern Alaska, south because troll fisheries for these fish are subject to minimum size regulations.

Among ocean regime periods, significant correlations were most common among the size and abundance of chum, pink, and sockeye salmon following the 1976–77 ocean regime change to 1994. We chose 1994 as the end of the period following the ocean regime change because size of chum salmon in the two North America populations monitored by Helle and Hoffman (1998) started to increase about that time. During 1977–94 correlations indicate that chum, pink, and sockeye salmon compete for resources in the ocean.

Our results indicate that some North American and Asian salmon populations may compete for resources in the ocean. Correlations between body size of chum salmon and abundance were higher when compared to the total of North American and Asian chum salmon than when compared to only the North American abundance. Correlations between the body size of chum and pink salmon abundance were more significant and negative when compared with the North American catch, than with the total Pacific catch. However, body size of pink salmon from central and southeast Alaska were strongly related to abundance of total Pacific catch of chum salmon but not to the North American catch of chum salmon (Tables 1 and 2). The same comparisons with sockeye salmon were mixed. However, body size of sockeye salmon was more negatively related to the abundance of chum salmon in the total Pacific catch than to the catch of chum salmon in North America. Specifically, some North American chum and pink salmon are likely competing for resources in the ocean with Asian chum salmon, but not with Asian pink salmon. Body size of chum, pink and sockeye salmon were only occasionally related to the abundance of coho salmon.

Significant relationships between body size of chum and sockeye salmon and abundance of Chinook salmon were positive in 1960–76 and during 1977–94. However, in 1995–2005 the few relationships that were significant with Chinook salmon were negative (Tables 1 and 2). It is not likely that in 1995–2005 chinook salmon influenced the body size or abundance of chum, pink, or sockeye salmon because of the small numbers of Chinook salmon in the ocean.

We identified three time periods in the North Pacific Ocean between 1960 and 2006 which differ in the abundance of Pacific salmon and in terms of density-dependence. The first period was between 1960 and 1976. The abundance of Pacific salmon was low, and the effect of density dependence on the fish was the lowest. In the second period from 1977 to 1994, salmon were numerous and the effect of density on the body size of salmon was significant in many cases. The third period was between 1995 and 2006. The abundance of salmon remained high, however, the body size of the salmon was not commonly related to population density. This latter time period seems to be the most favorable for salmon. The ocean resources during this time supported salmon of large body size and large population numbers. We conclude that the carrying capacity of the North Pacific Ocean for producing Pacific salmon is not a constant value. Carrying capacity varies with changing environmental and biological factors.

ACKNOWLEDGMENTS

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Density-Dependent Growth of Sockeye Salmon in the North Pacific Ocean

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Abstract: Length measurements were obtained for sockeye salmon from several major rivers around the perimeter of the North Pacific Ocean. The salmon from the Kvichak River in Bristol Bay, Alaska exhibit strong cyclic changes in abundance, usually with a period of 5 years. The lengths of salmon show the same cyclic changes but are inversely related to the magnitude of salmon abundance. The same relationship was found for all streams in Bristol Bay. The strength of this association was measured by the correlation coefficients between the same age-classes in other districts. High values were interpreted as occupation of overlapping feeding areas by each age-class during the last year in the ocean before salmon reach full maturity. There was some overlap in feeding areas of salmon from neighboring districts such as the Copper River and the Karluk/Chignik watersheds in Alaska. No association was found between Bristol Bay sockeye salmon and their counterparts in either Russia or the Fraser River, British Columbia, Canada.

Keywords: sockeye salmon, length measurements, feeding migrations

BACKGROUND

Workers in the commercial canning industry in Bristol Bay, Alaska, have been well aware that the average length and weight of sockeye salmon (*Oncorhynchus nerka*) changes periodically. During peak years of the sockeye salmon in the Kvichak River, Bristol Bay, Alaska, one or two additional salmon were always required to produce a 21.8-kg case of processed fish than in off-peak years because the sockeye are consistently smaller during peak years. This is illustrated in Fig. 1, which shows the inverse relationship between abundance of sockeye salmon and the mean length of age 2.2 females. However, no one related the smaller fish size to limits in the carrying capacity of either the open ocean or coastal waters.

With the resumption of high seas fishing for Pacific salmon by Japan after the end of WWII, it became important to identify and understand the migration paths and continent of origin of the salmon being caught. The first large-scale tagging experiments were conducted by the Fisheries Research Institute at University of Washington. The salmon were caught in a large purse seine, the mouth of which was kept open for half an hour facing the direction of the surface currents. Salmon were never caught during the opening set. This observation demonstrated the important fact that juvenile salmon drift along with the surface currents. The fourth

dimension, time, must therefore be added to the geometric coordinates at place of tagging. A first model of the ocean drift of sockeye salmon was given by Royce et al. (1968).

Other tagging experiments followed, conducted by the nations bordering the North Pacific Ocean. In an effort to summarize our knowledge French and Bakkala (1974) presented a model of the oceanic migration of Bristol Bay sockeye salmon. However, the number of tags recovered from the commercial fishery and spawning ground surveys remained small. Another important step was to identify the place of origin of all high seas salmon through genetic analysis (Habitcht et al. 2005).

Each salmon carries a bit of its oceanic history in the pattern of its scales. Many retrospective studies of scale collections have been made over the years. When optical scanning methodologies were developed, scale analysis became an important tool to understand the life history of salmon (Isakov et al. 2001). Another step in this developmental process was to consider numbers and widths of individual scale rings (Ruggerone et al. 2005).

Another approach to understanding the ocean life of sockeye salmon is to study parameters such as survival rates of returning fish. Peterman et al. (1999) analyzed the covariance between adjacent sockeye salmon stocks in the Fraser River, BC, and those in Bristol Bay, Alaska. He concluded that there was no connection between sockeye in either river
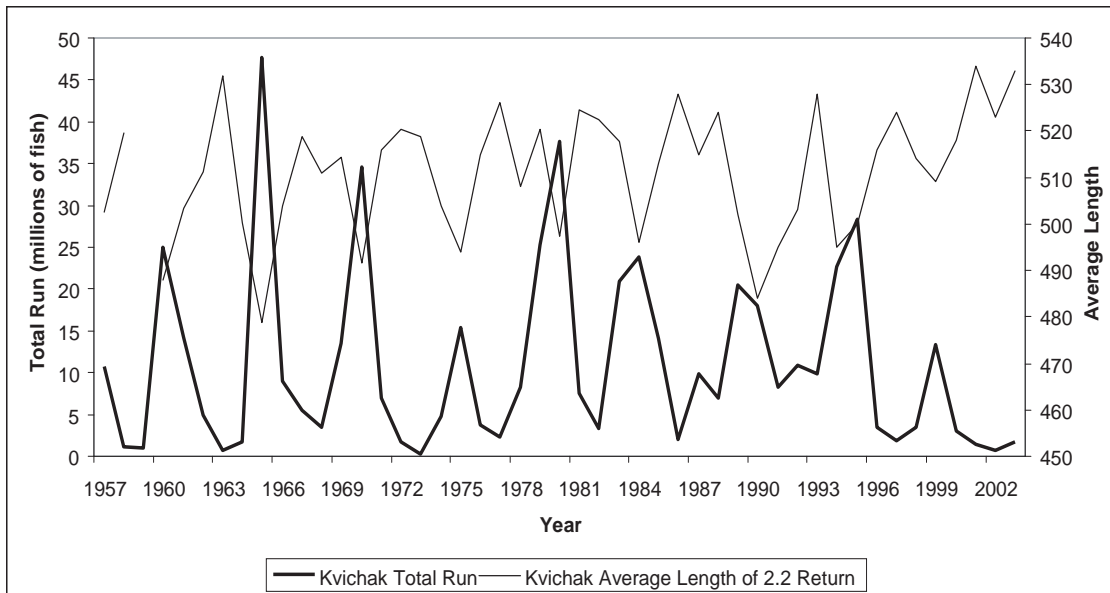
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Fig. 1. The inverse relationship between the magnitude of sockeye salmon run to the Kvichak River, Bristol Bay, Alaska, and the mean length of age 2.2 females. Time period covered 1957 to 2003.

system. In the present study we compare the mean lengths of the various stocks of sockeye salmon to determine the relationships between various populations.

MATERIALS AND METHODS

The data for this study were obtained from the archives of many research institutions around the Pacific Rim that are managing and monitoring salmon resources. Sockeye salmon are distributed from the southern tip of the Kamchatka Peninsula through watersheds along the North Pacific coastline, including the Bering Sea, to the southern border of the state of Oregon. Small populations are occasionally found south of these two endpoints on both sides of the North Pacific Ocean (Fig. 2).

From this wide area, we selected stocks from several rivers for this study. The choices were based on importance to the salmon fishery within particular areas but also on the availability of data (Table 1).

The majority of rivers examined in this study are located
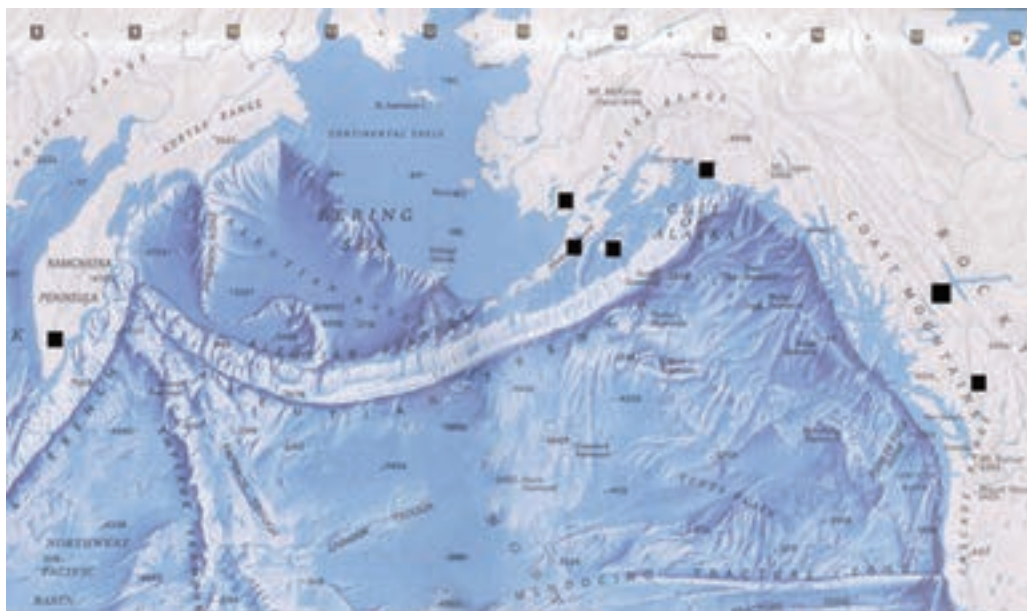

Fig. 2. Map of the North Pacific Basin and the Bering Sea with sites of collection of measurements. Locations—West to East: Kamchatka Peninsula, Bristol Bay, Chignik River, Karluk River, Copper River, Skeena River and Fraser River.

Table 1. Summary of locations and rivers with available measurements.

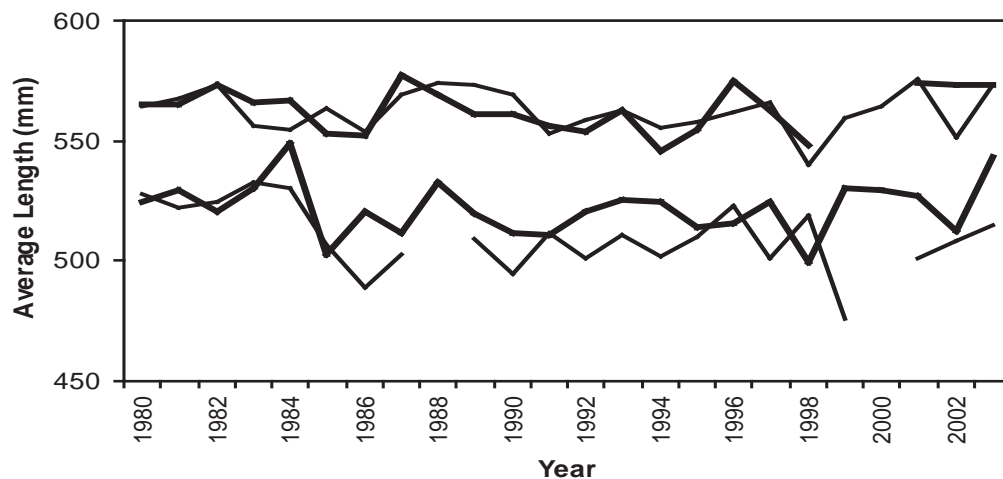| Area	Rivers and lakes	Measurement
Russia	Ozernaya & Kamchatka rivers	Standard Length
Chignik	Chignik River	ME – FT
Karluk	Karluk River	ME - FT
Bristol Bay	All	ME – FT
Prince William Sound	Copper River & Eshamy Lake	ME – FT
British Columbia	Skeena and Fraser rivers (Cultus Lake, Adams River & Chilko Lake)	Standard Length

Fig. 3. Mean lengths of age 2.2 (bottom) and 2.3 (top) sockeye salmon in the catch (heavy line) and escapement (light line) in the Togiak River, Bristol Bay. The breaks in lines indicate missing data.

within the state of Alaska. Bristol Bay contains the heaviest concentration of spawning sockeye and the broadest extent of spawning grounds and rearing areas. We also studied sockeye from the Fraser River, BC, an area with many large stocks of spawning sockeye salmon.

Most of the data are based on measurements taken from mid-eye (ME) to the fork of the tail (FT) of the fish. By taking measurements along the skeletal structure it is possible to compare salmon from different spawning grounds, thus avoiding the problems introduced as a result of sexual dimorphism in salmon caught in the commercial fishery. Equations to convert from one type of length measurement to another were developed by Duncan (1956). Originally it was hoped that length measurements could be used to identify different salmon races, but this turned out not to be possible. The other measurements were standard length (from the tip of the snout to the fork of the tail). Wherever possible, comparisons are based on measurements of females.

The salmon return in a year at different ages. The most common freshwater ages are 1. and 2. following the notation of Koo (1962). There are a few streams where 0. sockeye are common while in other streams 3. salmon are encountered. However, each of these groups is small in number and not

included in this study.

We see a similar pattern for sockeye salmon differing in saltwater age. Two groups, .2 and .3, (two- and three- sea-year, respectively) form the major part of a year's returns. Jacks (or .1 salmon) are not retained by the gill nets in use today. They represent a small fraction of salmon returns and are not included in this study.

RESULTS

Net Selectivity

Most length measurements of sockeye salmon in Alaska were from fish seined at river mouths. These salmon had first to pass through the corresponding fishing district. Linen gill nets were in use from the inception of the fishery in the 1880s to the 1950s. During this time period the mesh size decreased from 6 ¼" stretched mesh to 5 ½". The old nets were highly selective for size and retained larger fish, especially males (Mathisen 1971).

Since the mid fifties monofilament nylon gill nets with a stretched mesh size of 5 3/8" have been used in Alaska. In order to compare the length distributions obtained in the
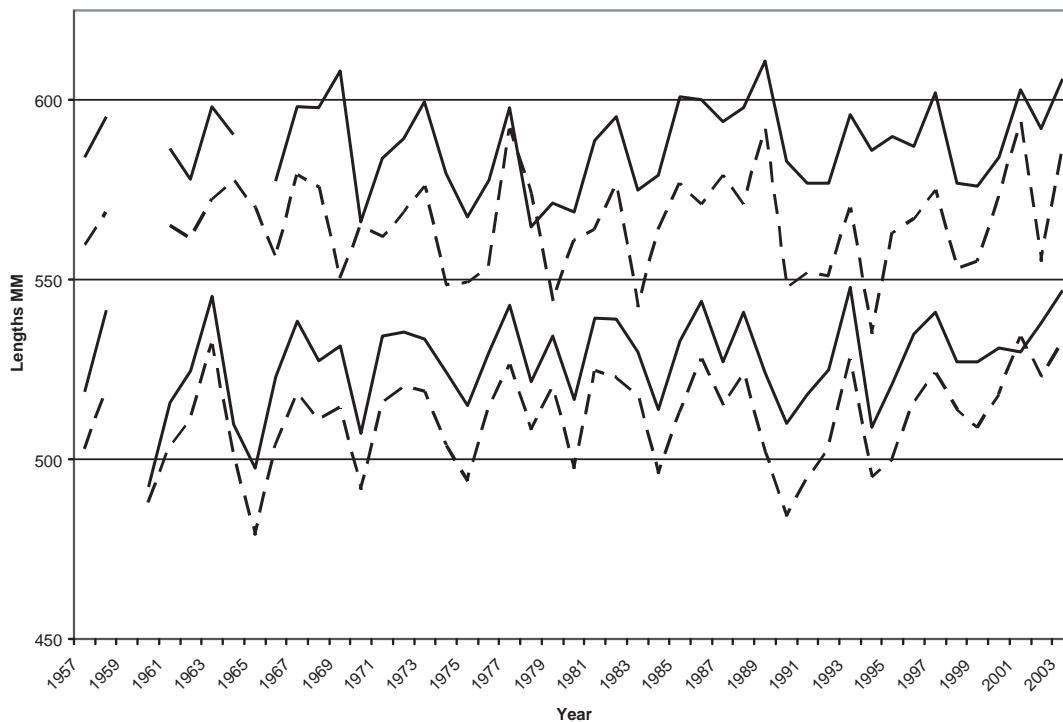
Fig. 4. Mean lengths of male (solid line) and female (broken line) sockeye salmon from the Kvichak River in Bristol Bay. Top: age 2.3; bottom: age 2.2.

commercial fishery with escapement numbers we selected the Togiak River in Bristol Bay. It is the most westerly major river in Bristol Bay with a commercial fishery. There is no possibility that sockeye salmon from the other rivers in this study could be mixed with the Togiak salmon. As seen in Fig. 3, the length distribution observed in the commercial fishery and that obtained in the escapement from the Togiak River do not indicate any size selectivity for 2.3 fish (a pair-wise t-test gave a value of $P = 7681$). For the 2.2 sockeye there is a significant value ($P = 0.004$). It should be remembered that we had no means to sort out the sampling error. With this reservation, we decided to treat the mean length distributions from escapement data as interchangeable with mean length distributions for the entire stock. This provided the advantage of using the length distribution from a homogenous stock of salmon, not from a mixed stock, which is the case in the commercial catch. Thus, we conclude that for this study the mean lengths in the escapement data are representative of the total run.

Variation in Length

Comparison of the Kvichak River Age/Sex Groups of Sockeye Salmon

Figure 4 shows a comparison of age groups, 2.2 and 2.3, for males and females. The difference in mean length between males and females of the same age varies from one to two centimeters. Some years show a larger spread between the sexes, which might be the result of sample vari-

Table 2. Pearson correlation coefficients in length between sockeye salmon sexes by age group in the Kvichak River, Bristol Bay.

Age-class	Correlation	Sample size	Significance
1.2	0.75	40	$P < 0.01$
1.3	0.75	40	$p < 0.01$
2.2	0.93	47	$P < 0.01$
2.3	0.63	47	$P < 0.01$

ability. Likewise, there is a larger spread (5–6 cm) in length between .2 and .3 fish of either sex. There is more variability in age .3 between the two sexes than for the age .2 fish. A comparison of the correlation coefficients for males and females for the principal age-classes are shown in Table 2.

There is a high correlation between males and females for all age groups, especially age group 2.2. The correlation coefficient is as high as one would expect from visual inspection of the graph. On this basis we conclude that males and females are mixed together during ocean residence, or at least during the final year before they return to spawn.. We use the magnitude of the correlation coefficients as a measure of overlap in feeding areas.

Comparison of Streams in Bristol Bay

We compared length distributions of sockeye salmon from the Kvichak River and the nearby Naknek River in
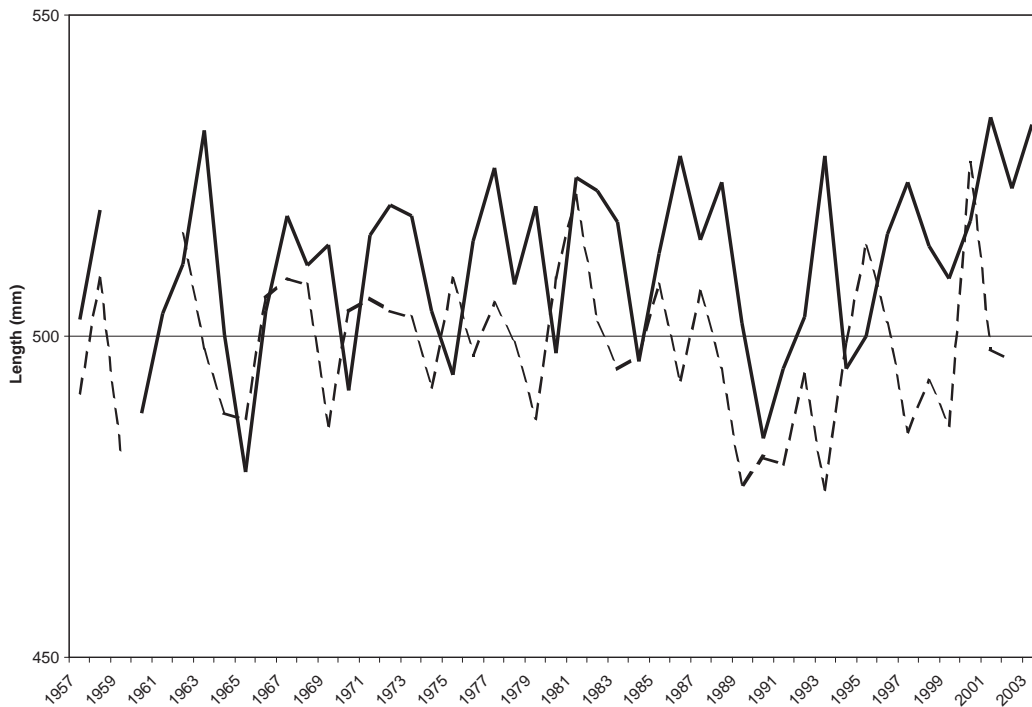
Fig. 5. Mean lengths of female sockeye salmon (age 2.2) from the Kvichak (solid line) and Naknek (broken line) rivers in Bristol Bay.

Table 3. Pearson correlation coefficients between the mean length of sockeye salmon in the Kvichak River and other rivers in Bristol Bay. Significant (α = 0.05) relationships are noted in bold and italics. Sample size is 42 in each case.

River	Age-class	
	2.2	2.3
Naknek	*0.66*	*0.58*
Egegik	*0.54*	*0.32*
Ugashik	*0.59*	0.28
Igushik	0.12	*0.49*
Wood	0.27	*0.44*
Togiak	-0.03	*0.30*

Bristol Bay. We saw similar fluctuations in mean length in both rivers (Fig. 5 and Table 3). The cyclic fluctuations are less pronounced in the Naknek River. Historically, the production of sockeye salmon in the Naknek River, measured in numbers, has been much more stable than in the larger Kvichak River. The regression coefficients for Kvichak Bay and the Egegik and Ugashik rivers are high for age 2.2, and also for age 2.3, although less so. In the Igushik, Wood and Togiak rivers there is no significant correlation for age 2.2 but a significant correlation for age 2.3 salmon. This could be interpreted that .3 fish have an extra year to travel out of or into feeding areas for salmon from different rivers.

There are variations within such a large number of salmon stocks. A comparison with a large river system such as the Wood River demonstrates this variability. In Fig. 6, the mean length of females age 2.2 for the Wood River is more out of phase than in phase with the corresponding curve for the Kvichak River females of the same age. But when the mean length for females age 2.3 is plotted, the two graphs are more synchronized (Table 3).

We conclude that despite noted discrepancies, the sockeye salmon from the various rivers in Bristol Bay have many growth features in common such that they can be dealt with as a single unit.

Comparison of Districts

We compared mean lengths for Kvichak River age 2.2 females and Copper River (Prince Williams Sound) age 1.2 females. This choice was necessitated because the 2.2 age-class of Copper River sockeye is not abundant (Fig. 7). There are fluctuations in mean length over time for the Copper River fish, but they are small compared to the Kvichak River fluctuations. Further, they are not well synchronized with the Kvichak salmon run. It should be noted that there is a significant correlation coefficient between age 1.2 fish from the Copper River and age 2.2 fish from the Kvichak River, which suggests overlapping feeding grounds between the numerically strong Kvichak run and the much smaller Copper River run. We suggest that this took place closer to the Copper River sockeye salmon feeding grounds and therefore represents a tentative eastern boundary for the Bristol Bay salmon.
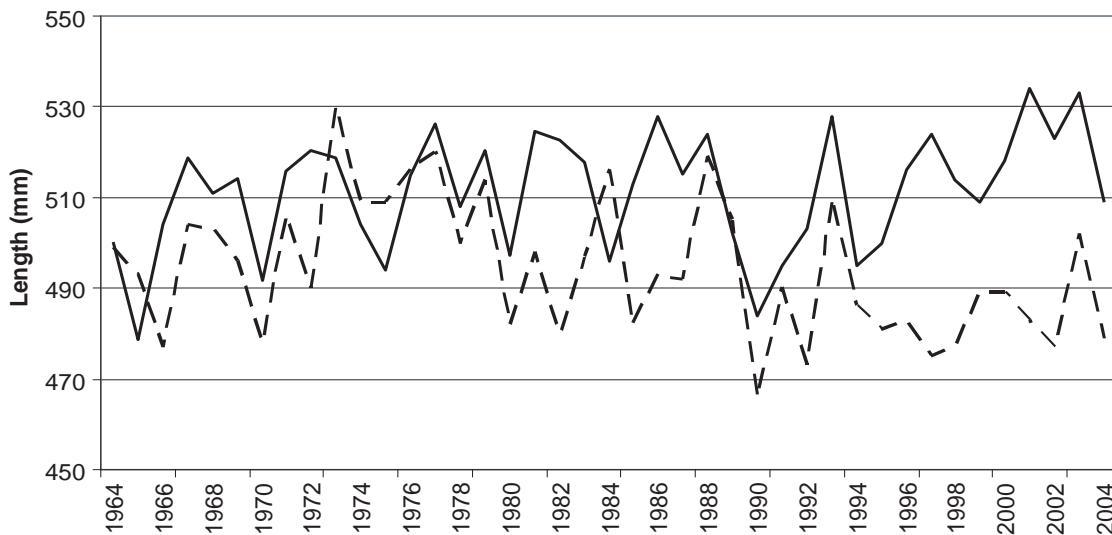
Fig. 6. Mean lengths of female sockeye salmon (age 2.2) from the Kvichak (solid line) and Wood (broken line) rivers in Bristol Bay.
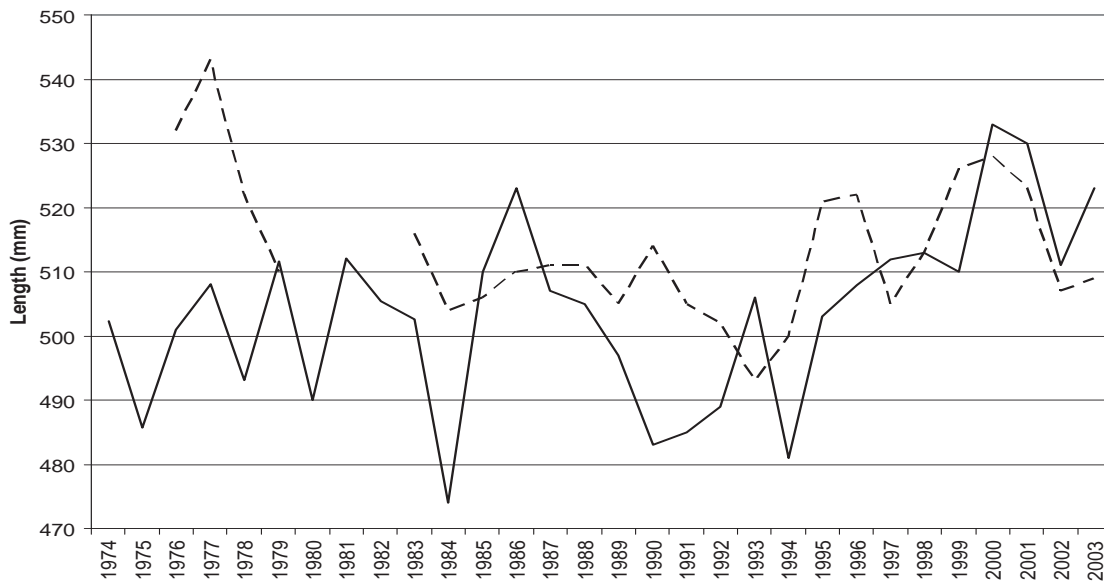

Fig. 7. Mean lengths of female sockeye salmon (age 1.2) from the Copper River (broken line) in Prince William Sound and the Kvichak River (solid line) in Bristol Bay.

We then compared the sockeye salmon runs to the Chignik River in Alaska Peninsula and the Karluk River on Kodiak Island (Fig. 8). The amplitudes of the oscillations are smaller than seen elsewhere with the two graphs in phase during 1986–2004. Still, it is important to note that the age-class 2.2 in both rivers failed to produce significant correlation coefficients with the Kvichak 2.2 females, while the 2.3 salmon in both rivers had significant correlation values.

We have length measurements from two major rivers on the Kamchatka Peninsula, the Kamchatka and Ozernaya rivers. The measurements have been combined in Fig. 9. These graphs show that a 1. or a 2. freshwater life history does not affect the final length at maturity. There are pronounced cyclic changes in the length measurements, with lengths of the females increasing by up to 5 cm from peak to off-peak years. The data show no indication of overlapping feeding grounds such as those shown for Bristol Bay sockeye (see Table 3). This is in line with the annual north–south migrations of the sockeye salmon in the Far East (Radchenko and Mathisen 2004).

The Adams River and Chilko Lake, British Columbia, represent two spawning locations that are geographically distant from each other. Nevertheless, a plot of the mean lengths of these two populations shows that they vary synchronously. Because we assume that synchronous changes in mean length indicate overlapping feeding areas (Fig. 10), we
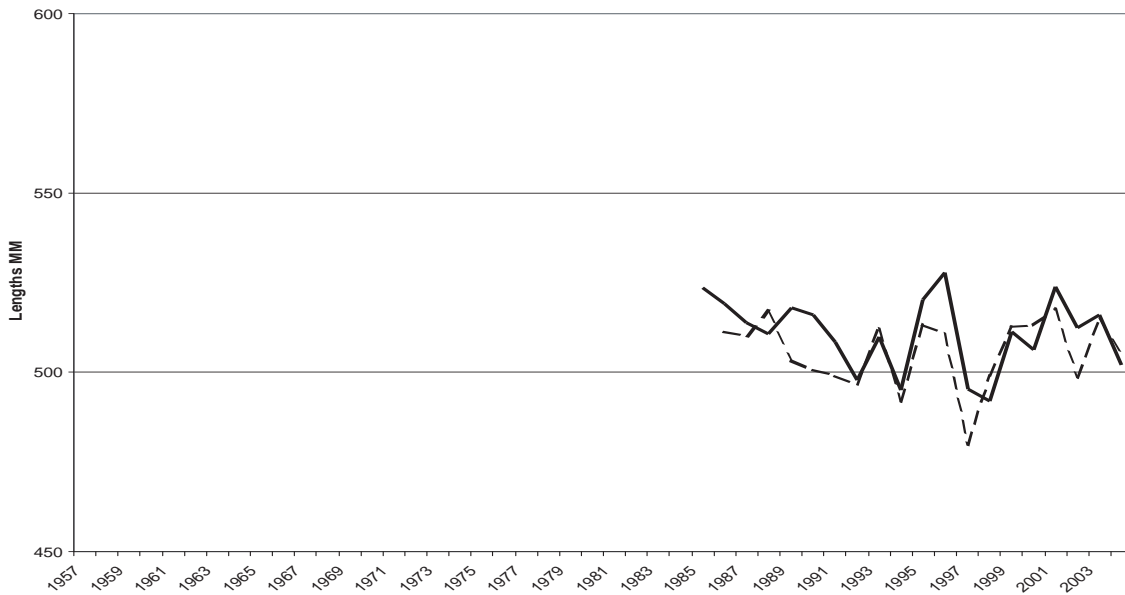
Fig. 8. Mean lengths of female sockeye salmon (age 2.2) from the Karluk River (broken line) on Kodiak Island and the Chignik River (solid line) in Alaska Peninsula.
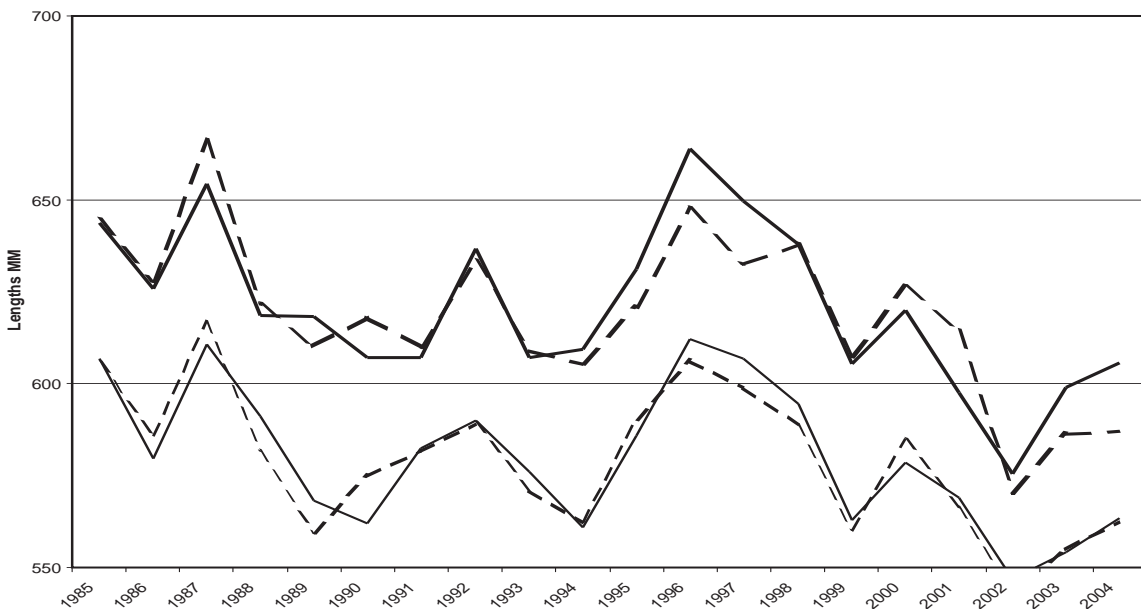

Fig. 9. Mean lengths of male (top) and female (bottom) sockeye salmon from the Kamchatka and Ozernaya rivers in the Kamchatka Peninsula, Russia. Solid lines: age 2.3; broken lines: age 1.3.

then examined the correlation coefficients. The low correlation coefficients (compared to those for the Kvichak salmon, e.g.) suggest that there is no overlap in ocean feeding areas.

There are some indications in Fig. 11 that the mean lengths of Cultus Lake sockeye decline toward the end of the time series. In the Bristol Bay data and elsewhere there is no indication that the mean lengths are declining. If this reduction in mean length was caused by a lowering of ocean productivity, a reduction in mean size would manifest itself at all locations. Hence we suggest that competition for food

resources is a major cause.

We have length measurements from the Skeena and Fraser rivers, British Columbia. The Fraser River has the second largest concentration of sockeye salmon in North America, after Bristol Bay. There are a number of different spawning populations. Two of them have been selected and their mean lengths plotted in Fig. 12. This is the longest time series in this study.

The Skeena River lies north of the Fraser River complex (Fig. 2). Salmon in the two rivers differ in age composi-
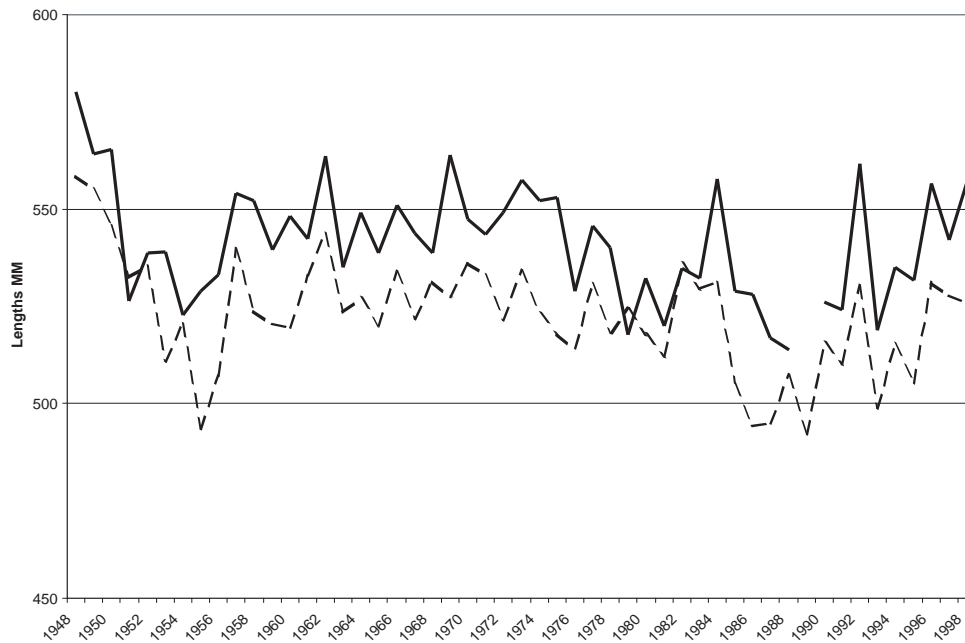
Fig. 10. Mean lengths of female sockeye salmon (age 1.2) from the Adams River (solid line) and Chilko Lake (broken line) in British Columbia.
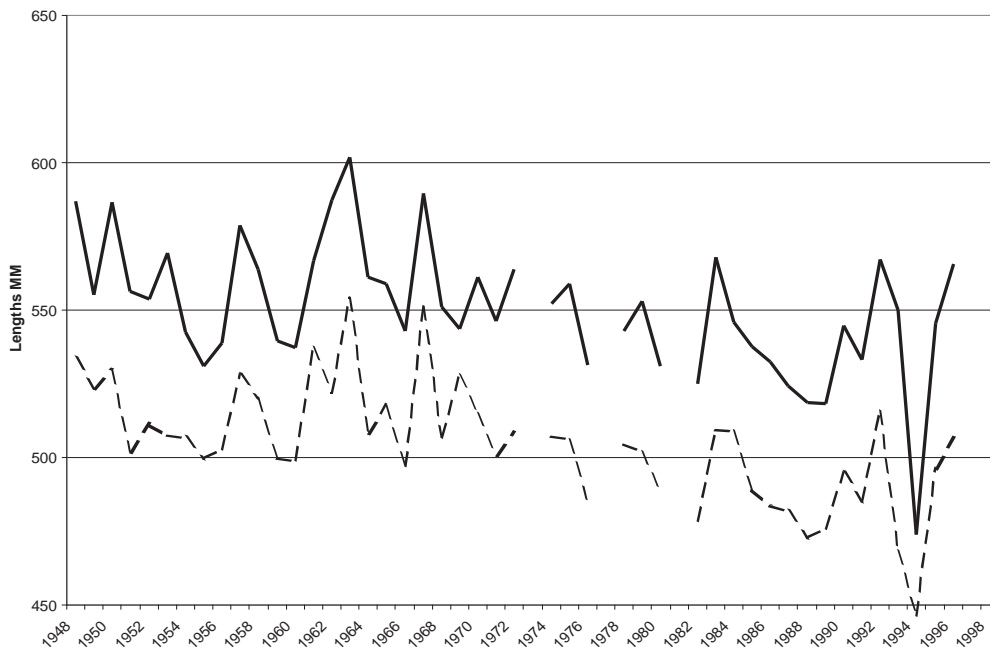
Fig. 11. Mean lengths of male (solid line) and female (broken line) sockeye salmon (age 1.2) from Cultus Lake in British Columbia.

tion and fish having two freshwater annuli are very common in the Skeena River. The mean lengths of .2 and .3 ocean salmon have been plotted in Fig.12. There is no indication of cyclic changes in mean length. The complete geographical segregation of the Fraser and Skeena river systems is shown in Tables 5a and 5b where the correlations coefficients have been calculated. There are no significant relationships between the mean lengths of sockeye in the two river systems.

DISCUSSION

The Structure of Sockeye Salmon Foraging in the Ocean

This study reports on measurements of sockeye salmon from a variety of spawning locations over many years. These time series have been used to make some inferences about the structure of sockeye salmon feeding in the North Pacific Ocean. The underlying assumption is that salmon

Fig. 12. Mean lengths of age 2.2 (heavy line) and 2.3 (light line) sockeye salmon from the Skeena River in British Columbia.

Table 4. Pearson correlation coefficients between the mean length of female sockeye salmon from the Kvichak River and other rivers. Significant (α = 0.05) relationships are noted in bold and italics. Sample sizes are indicated in parentheses.

River	Age-class		
	1.2	2.2	2.3
Karluk		0.18 (20)	*0.67* (20)
Chignik		0.37 (19)	*0.52* (19)
Chilko	-0.23 (26)		
Adams	-0.22 (26)		
Cultus	0.11 (26)		
Eshamy	-0.15 (21)		
Copper	*0.50* (21)		
Ozernaya (Kamchatka Pen.)		0.02 (15)	0.26 (15)
Kamchatka early run			0.10 (20)
Kamchatka late run			0.10 (20)

Table 5a. Relationship to Skeena River and selected stock in the Fraser River (Female 1.2).

	Skeena	Cultus	Adams	Chilko
multiple r		14.8%	-2%	10%
p-value		0.53	0.93	0.66
significance		no	no	no
stationary mean	yes	yes	yes	yes

Table 5b. Relationship to Skeena River and selected stock in the Fraser River (Male 1.2).

	Skeena	Cultus	Adams	Chilko
multiple r		23%	36%	22%
p-value		0.31	0.09	0.3
significance		no	no	no
stationary mean	yes	yes	yes	yes

showing the same growth pattern in the final year of ocean residence must have been feeding together in the ocean during this time.

The length measurements demonstrate two growth patterns. In some cases there is a slow but steady decline with time in average length. The more common mode involves cyclic changes in final length at maturity corresponding to the underlying cycle. The sockeye salmon in Bristol Bay serve as an example.

The seaward migration of smolts takes place toward the end of May and the first part of June. During a time span of 2–3 weeks in excess of half a billion smolts pour into Bristol Bay. Here their migration slows down as they move westward along the Aleutian Chain or over the lower shelf in the Bering Sea (Straty 1975; Jewett et al. 2004; Farley et al. 2005). As fall arrives the juvenile sockeye salmon apparently move south of the Aleutian chain in a manner similar to the Russian sockeye salmon along the eastern coast of Kamchatka (Radchenko and Mathisen 2004). Immature salmon in the age groups .1 or .2 are seldom captured during an-

nual surveys intended for .0 juveniles (E. Farley, Auke Bay Laboratory, Alaska Fisheries Science Center, 11305 Glacier Highway, Juneau, AK 99801-8626, pers. comm.)

During this feeding phase in the life of the sockeye salmon there are ample opportunities for the various stocks to mix. We know that this is true for the Bristol Bay salmon feeding on the high seas. Toward their final year in the sea, the maturing salmon assemble in the coastal waters where in peak years competition for food must be severe as evidenced by a loss of 3 to 5 cm in final length compared to the average length in off-peak years. Ruggerone et al. (2003) have studied the growth of sockeye salmon from the Kvichak and Egegik rivers. Their average scale growth curves show a substantial increase in length (and therefore in weight) during the last year of ocean residence.

In short, the smolts migrate to sea and spread out like a fan, which will close in a counter- clockwise fashion with the onset of winter and bring the juveniles south of the Aleutian Chain. Until maturity the sockeye salmon remain in the current system so time becomes an important factor in addition to the geographic coordinates. The areas serving as nursery grounds presumably will expand or contract according to the total biomass of sockeye salmon. There are distribution maps in the literature, which probably represent maximum expansions.

Although the time series of size for the northern Gulf of Alaska rivers (such as the Copper River) are shorter than for Bristol Bay rivers, only the youngest of the returning fish mix with Bristol Bay salmon, whereas the .3 ocean fish are isolated from the Bristol Bay sockeye judging from the correlation coefficients in Table 3. The Copper River could be considered as the eastern extension of the Bristol Bay sockeye salmon complex.

In regard to the Karluk/Chignik complex, the two curves in Fig. 8 are very similar, as expected from the proximity of the two rivers. Judging from the correlation coefficients the Karluk/Chignik populations do not mix with the Bristol Bay salmon. For the .3 ocean salmon we find that these fish do mix with the Bristol Bay salmon (Table 4). This is the same behavior pattern as observed for the Nushagak River sockeye salmon. One could perhaps use the westward expansion as the limit of the area occupied by the Bristol Bay sockeye salmon complex.

The geographical boundaries of Bristol Bay sockeye salmon should not be considered as solidly fixed. We are dealing with probabilities, and total number of fish becomes one of the governing parameters. The net impression is that the Bristol Bay sockeye salmon travel and feed throughout their life as a homogeneous unit. The sockeye salmon in the Fraser River system do not mix with Bristol Bay salmon as indicated by Peterman et al. (1998) and demonstrated by our length measurements and correlation coefficients. Further, the sockeye salmon from the Kamchatka Peninsula do not mix with their counterparts farther east. Given the rapid advances in genetic identification, we will soon be able to identify the place of origin of juvenile sockeye salmon intercepted on the high seas (Habicht et al. 2005).

Carrying Capacity of the North Pacific Ocean

Recently there have been many reports that claim that the average length of chum salmon is decreasing, and that changes in age composition are occurring (Ishida et al. 1992; Kaeriyama 1998, 2003; Helle and Hoffman 1995, 1998). Some think that these observations are related to changes in climate which, in turn, may have altered the productivity of oceanic nursery grounds. Another more plausible cause is that the carrying capacity of the ocean area in question has been reached or even exceeded. This could be caused, in part, by the rapid expansion of ocean ranching of chum salmon by Japan.

For sockeye salmon it is clear that the ecosystem cannot support runs much larger than those seen today during peak years. High spawning density results in reduced growth of fry. This, in turn, will reduce the survival of the juvenile sockeye salmon feeding in the sea. A self-regulating mechanism of this kind will place an upper limit on the number of spawners that a river can support.

In the Fraser system which has the longest record of measurements to date, we do not find pronounced changes in total length. On the other hand, in streams such as the Stuart and Nadina we see a sharp decline in mean length with the time. In a few cases such as Cultus Lake there are signs of decreasing mean length. There could be a decline in the productivity of the oceanic ecosystem utilized by the sockeye salmon from the Fraser River. However, this would then have a universal character and not be confined to fish from just a few streams. On the other hand, there are man-generated changes to the ecosystems in the eastern part of the Gulf of Alaska. Ocean ranching of pink salmon has been very successful, especially in Prince William Sound. At the same time ocean ranching of the more valuable chum salmon is growing steadily. Helle and Hoffman (1998) report reduced growth and increased age at maturity of wild stocks of chum. There is enough overlap in dietary spectra among salmon to make this a plausible suggestion.

Cyclic Abundance in Sockeye Salmon

The magnitude of salmon runs to many different streams in different locations display cyclic changes in abundance. Figure 9 indicates a strong cycle in abundance for the two streams examined on the Kamchatka Peninsula. The cycle in the Kvichak River has been known since the inception of the fishery. Lately the peak years have been small in the Kvichak system, but at the same time the Egegik runs have been strong such that the total number of salmon returning to the eastern side of Bristol Bay has not changed significantly. There still is discussion about interception of Kvichak salmon in the Egegik District. In the Fraser River there

are many streams with cyclic patterns, in addition to that in the well-known Adams River. The year of peak abundance can shift depending upon the life history of the stock under consideration.

The reason for development of sockeye salmon cycles cannot be to increase production or biomass. As pointed out by Mathisen and Sands (2001) the increase in numbers is accompanied by a decrease in weight, leaving the total biomass without significant fluctuations. However, the increase in numbers has a drastic effect on the distribution of the escapement. In 1965, for example, the Kvichak escapement had close to 25 million spawners, with the result that spawners were found in unlikely locations such as over bedrock or rock falls. Clearly one function of a peak year in the salmon cycle is to deliver spawners to all possible sites in the nursery areas.

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A Review of the Critical Size, Critical Period Hypothesis for Juvenile Pacific Salmon

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Abstract: In this review, we consider size of juvenile Pacific salmon (*Oncorhynchus* spp.) after the first summer at sea to be the trait on which size-selective mortality operates. The idea is based on the critical size, critical period hypothesis, where those individuals within a cohort that do not reach a critical size during their first summer at sea have higher rates of late fall and over-winter mortality. The results suggest that early marine growth of juvenile Bristol Bay sockeye (*O. nerka*), Prince William Sound hatchery pink (*O. gorbuscha*), and British Columbia coho (*O. kisutch*) salmon from geographically distinct regions (Bering Sea, northern Gulf of Alaska, coastal British Columbia, respectively) is important and that these salmon must attain sufficient growth during their first summer at sea to survive subsequent years at sea.

Keywords: critical size, juvenile Pacific salmon

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) experience relatively high mortality rates during the first few months at sea (Parker 1968; Hartt 1980), and it is believed that the high mortality rates may be partly related to size (Pearcy 1992). Size-dependent marine mortality of juvenile salmon may be concentrated during two specific early marine life-history stages. The first stage may occur just after juvenile salmon enter the marine environment, where smaller individuals are believed to experience higher size-selective predation (Parker 1968; Willette et al. 1999). The second stage is thought to occur following the first summer at sea, when smaller individuals may not have sufficient energy reserves to survive late fall and winter (Beamish and Mahnken 2001). Thus, larger individuals within a cohort likely have higher probability of survival, emphasizing the importance of size during the first summer at sea.

In this review, we consider size of juvenile Pacific salmon after the first summer at sea to be the trait on which selective mortality operates. The idea is based on the critical size, critical period hypothesis, where those individuals within a cohort that do not reach a critical size during their first summer at sea have higher rates of late fall and over-winter mortality (Beamish and Mahnken 2001). Here, we briefly discuss two different methods to examine critical size (longitudinal sampling and retrospective analyses) for Pa-cific salmon and provide recent examples from the literature. In the next section, we examine the critical period concept by estimating marine stage mortality of juvenile Pacific salmon to determine the magnitude of over-winter mortality. Lastly, we provide examples of possible mechanisms affecting growth of juvenile salmon during their first year at sea.

RESULTS AND DISCUSSION

Evidence for Critical Size of Juvenile Salmon

Longitudinal Sampling

Ideally, comparisons of size distributions prior to and after the first winter at sea based on repeated measurements of size from the same population would best address size-selective mortality. This type of sampling, known as longitudinal sampling (Chambers and Miller 1995), provides a means to directly assess individual growth. Recent papers that employed longitudinal sampling utilized the fact that scale radius length is proportional to fish body length (Francis 1990; Ricker 1992) and compared average circuli spacing of first-year marine scale growth collected from juvenile and adult salmon within a cohort (Beamish et al. 2004; Moss et al. 2005). For example, mean intercirculi spacing for ocean-age-0 coho salmon (*O. kisutch*) was significantly smaller than the mean intercirculi spacing for ocean-age-1 fish from the same cohort (Beamish et al. 2004; Fig. 1) suggesting

that larger individuals within a cohort had higher marine survival. In another example, relative frequencies of scale radius length at various early marine circuli for Prince William Sound (PWS) hatchery pink salmon (*O. gorbuscha*) indicated that scale radii for surviving adult pink salmon were significantly larger than for juveniles from the same brood year and the same circulus (Moss et al. 2005; Fig. 2). Again, direct comparisons of size from a cohort of PWS hatchery juvenile pink salmon indicated that larger fish had higher marine survival. Because coho and pink salmon spend one year in the ocean, the mortality for the smaller fish within a cohort was believed to occur during late fall and winter.

Retrospective Analyses

According to the critical size, critical period hypothesis, the number of juvenile salmon reaching the critical size after the first summer at sea will vary, but the critical size should be more stable because it is likely a function of the intrinsic physiology of juvenile salmon (Beamish and Mahnken 1999). One way to test the critical size element of this hy-

pothesis is to examine inter-annual variability in a time series of fish size from a sample of ocean-age-1 salmon during spring or early summer, as these fish comprise the surviving population after the first winter at sea. An example of a time series (1972 – 2000) of fork lengths (mm) for ocean-age-1 chum (*O. keta*) and sockeye salmon (*O. nerka*) captured in the central Bering Sea during July aboard Japanese research cruises (Ishida et al. 2002) is shown in Fig. 3. There was no significant trend in size for either ocean-age-1 sockeye or chum salmon (Ishida et al. 2002). These data provide strong evidence of size-selective mortality during the first year at sea, especially given that these fish likely represent mixed stocks from western Alaska, Russia and Japan (chum salmon) and experienced vastly different ocean conditions during their first year at sea.

Another way to get size after the first year at sea for salmon is to examine scale radius length from the focus to the first marine annulus for scales taken from adult salmon. As mentioned above, scale radius length is proportional to fish body length for Pacific salmon, thus, measuring the distance (mm) from scale focus to the first marine annulus provides an index of size of the salmon after their first winter at sea. If salmon reach a critical size to survive their first winter at sea, then we would expect to see little variation in their size index, as the adult scale samples available for analysis only reflect those juvenile salmon that had attained sufficient size in order to survive to adulthood, and not those that died at sea (Crozier and Kennedy 1999). For example, analyses of time series of size after the first year at sea measured from adult Bristol Bay sockeye salmon scale samples indicated a constant mean and variance for time series of freshwater age-1.0 and -2.0 sockeye salmon with coefficients of variation for size of less than 4% (Farley et al. 2007). The authors speculated that the low variability in size after the first year at sea and the fact that the size of these fish after their first year at sea was not significantly related to survival was due to size-selective mortality during the first year at sea.

As an additional test of the critical size, critical period hypothesis, we used the time series of Bristol Bay sockeye salmon scale and smolt size data to test for differences in the size of smolts and juveniles after their first year at sea between freshwater age groups within a river system or among freshwater age groups between river systems. If size at the first ocean winter is related to survival, then we should see a decrease in the differences between smolt size at age and size after the first year at sea among and between river systems. To examine this concept, we first compared the mean fork length for Egegik River and Kvichak River age-1.0 and -2.0 smolts (Egegik – 28 years of data from brood years 1953–1998 with some missing years; Kvichak – 46 years of data from brood years 1953–1998; data provided by the Alaska Department of Fish and Game) between freshwater age groups (1.0 and 2.0) and river systems. Next, we compared differences in average size measured from adult scales between age-1.0 and -2.0 sockeye salmon after their
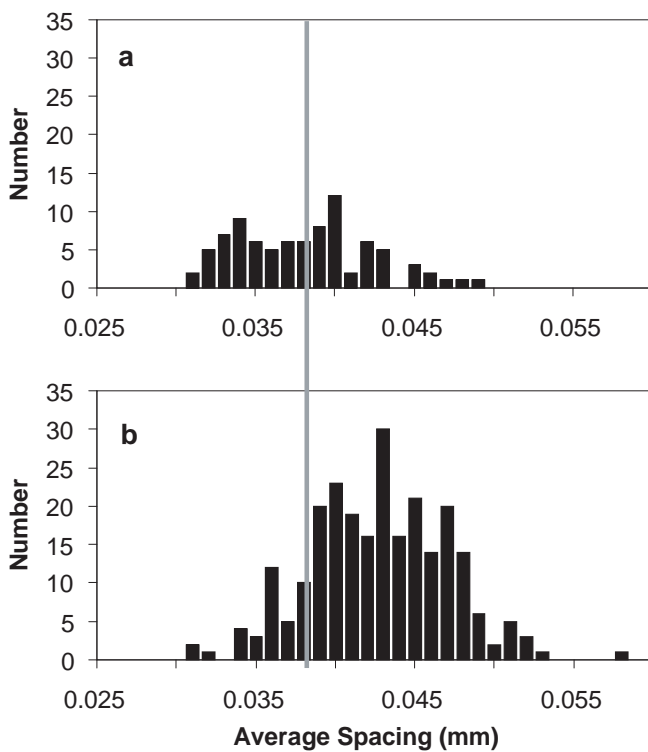
Fig. 1. The distribution of the average circuli spacing of the first 10 saltwater circuli from (a) ocean-age-0 coho salmon collected in the Strait of Georgia in September and November, 2000 (mean 0.038, SD 0.004; brood year 1998) and (b) ocean-age-1 coho salmon collected in March, July, August, and September in the Strait of Georgia and from Chilliwack and Big Qualicum hatcheries (mean 0.042; SD 0.004; brood year 1998). The vertical line through the histograms shows the mean intercirculi spacing for the ocean-age-0 sample in relation to the distribution of mean intercirculi spacing for ocean-age-1 fish, of which 82% are larger than the ocean-age-0 mean. (Figure from Beamish et al. 2004).

Fig. 2. Relative frequencies of scale radius length to circuli 3, 6, 9, 12, and 15 for hatchery pink salmon (dotted lines) and individuals of that cohort returning the following year as mature adults (solid lines) released by Armin F. Koernig (AFK), Cannery Creek (CCH), and Wally Noerenberg (WN) hatcheries in 2001 (brood year 2000). (Figure from Moss et al. 2005).
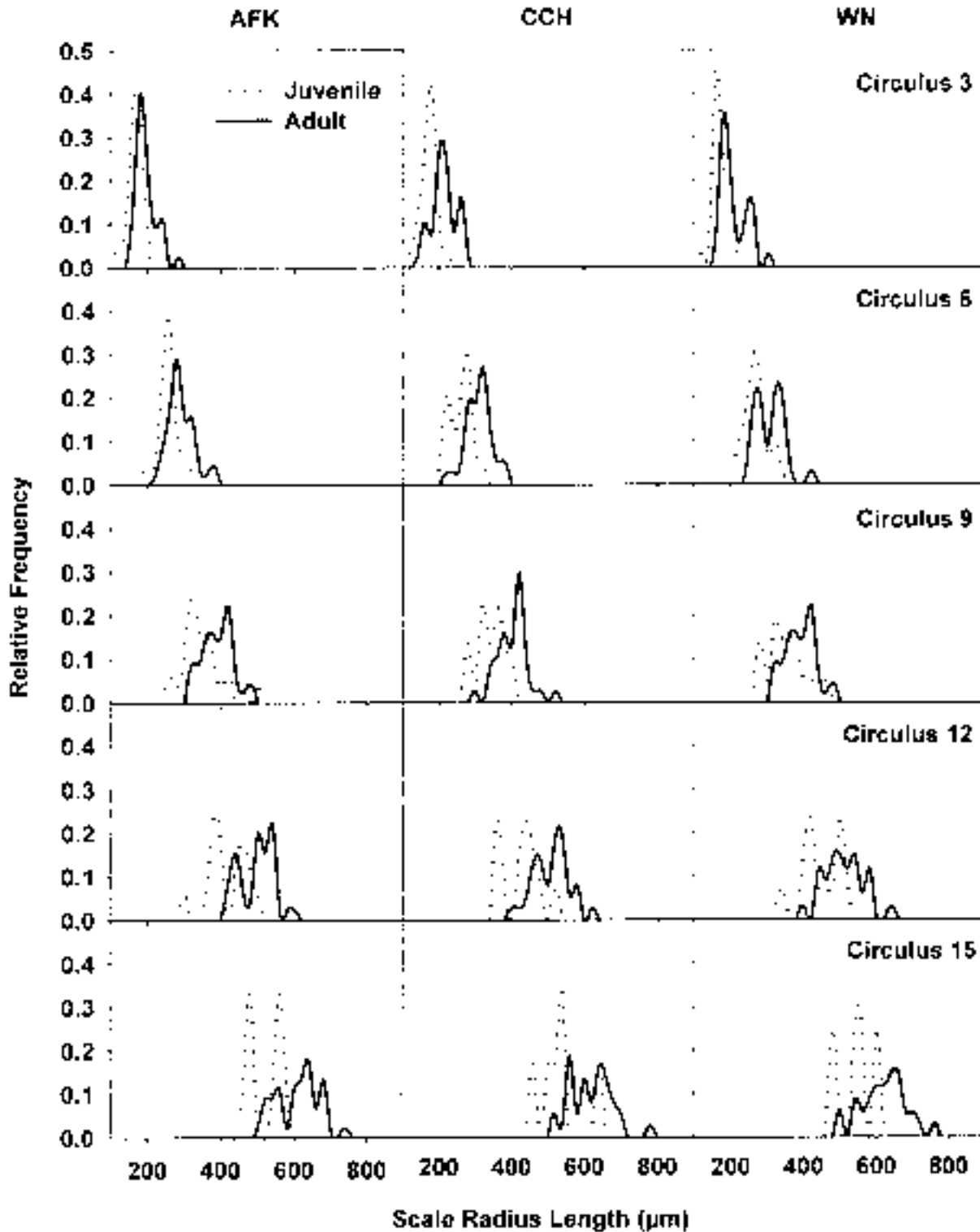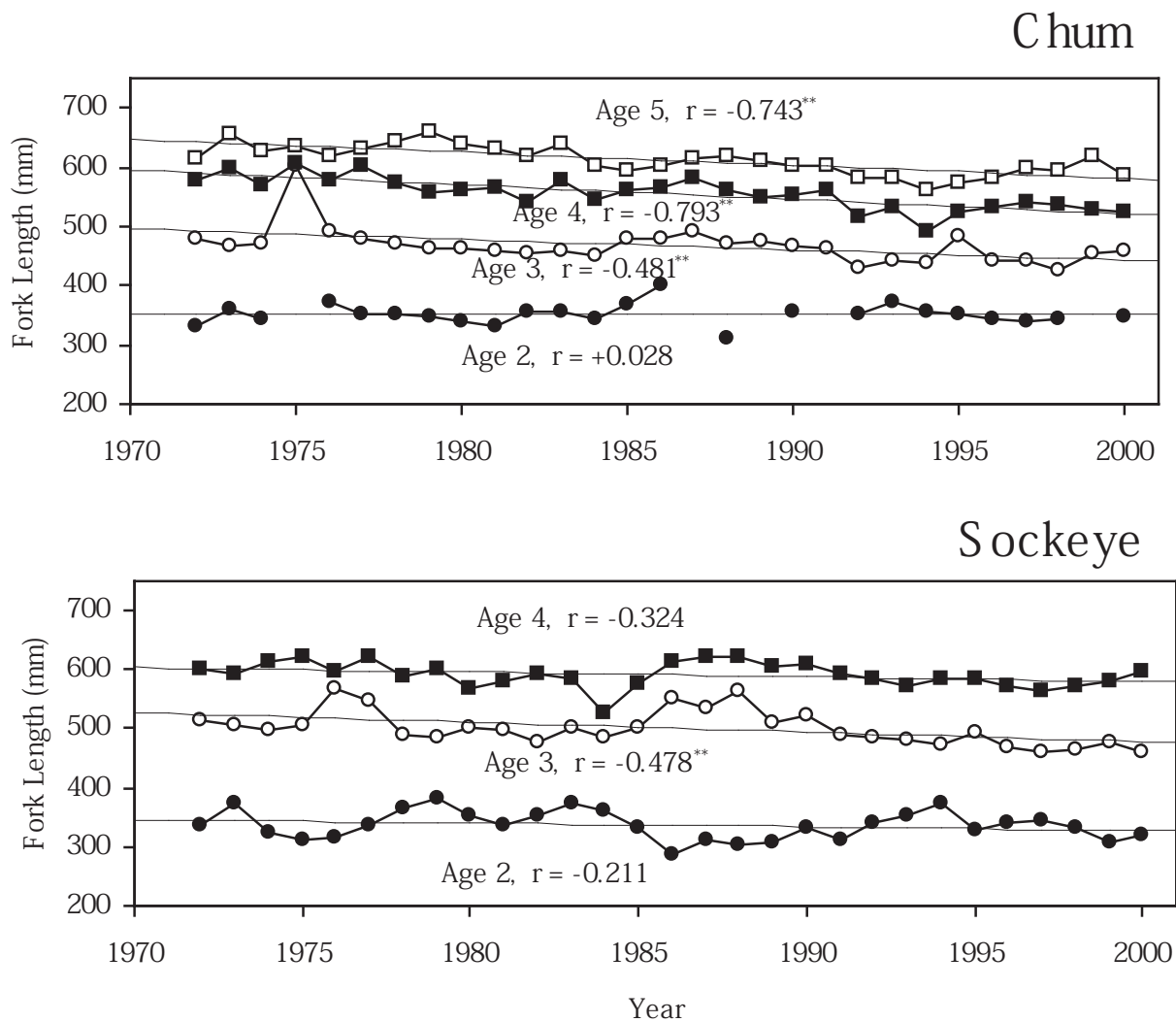
Chum

Sockeye

Fig. 3. Fork lengths (mm) of pink, chum, and sockeye salmon in the central Bering Sea in July from 1972 to 2000.   * significant at the 5% level; ** significant at the 1% level. Figure from Ishida et al. (2002). Note: age is designated as total age of the fish (i.e., Age 2 = "X.1 or 0.1", indicating size of the fish during July after their first year at sea (pers. comm., Y. Ishida, Ishiday@fra.affrc.qo.jp).

first year at sea. The results indicated that the average fork length of age-2.0 sockeye salmon smolts was 18.5% larger than age-1.0 smolts in the Kvichak River and 12.5% larger than age- 1.0 smolts in the Egegik River. The difference in mean size of juvenile sockeye salmon after the first year at sea between age groups and among river systems fell to 5.3% for the Kvichak River and 7.9% for the Egegik River. Comparisons in size among ages and between river systems indicated that age-1.0 and age-2.0 smolts were 19.6% and 11.9% larger in the Egegik River than in the Kvichak River. However after the first winter at sea, the differences between average size of Egegik River and Kvichak River smolts were reduced to less than 1% for age-1.0 fish and 2.8% for age-2.0 fish. These results suggest smaller age-1.0 sockeye salmon within and between river systems are either growing faster than larger age-2.0 sockeye salmon or that their mortality is much greater during their first year at sea. Evidence for

higher rates of mortality includes low survival of Kvichak River sockeye salmon with respect to other major sockeye salmon-producing river systems in Bristol Bay (Fair 2003).

Ricker (1962) proposed that marine survival of sockeye salmon increased with increasing smolt size. Henderson and Cass (1991) tested this idea for sockeye salmon from Chilko Lake located in the Fraser River, BC watershed.   There was no significant relationship between the mean length of smolts leaving the lake and the marine survival for brood years 1949 to 1985. However, adults returning to spawn had significantly larger scale-based indices of growth in fresh water than the corresponding smolts of the same brood year. This indicated that there was higher mortality for smolts that were smaller as indexed by their scale growth. Beamish and Mahnken (1999) published new data from the Henderson and Cass (1991) study that was an index of scale growth up to the first marine annulus (Fig. 4). The data in Fig. 4 repre-
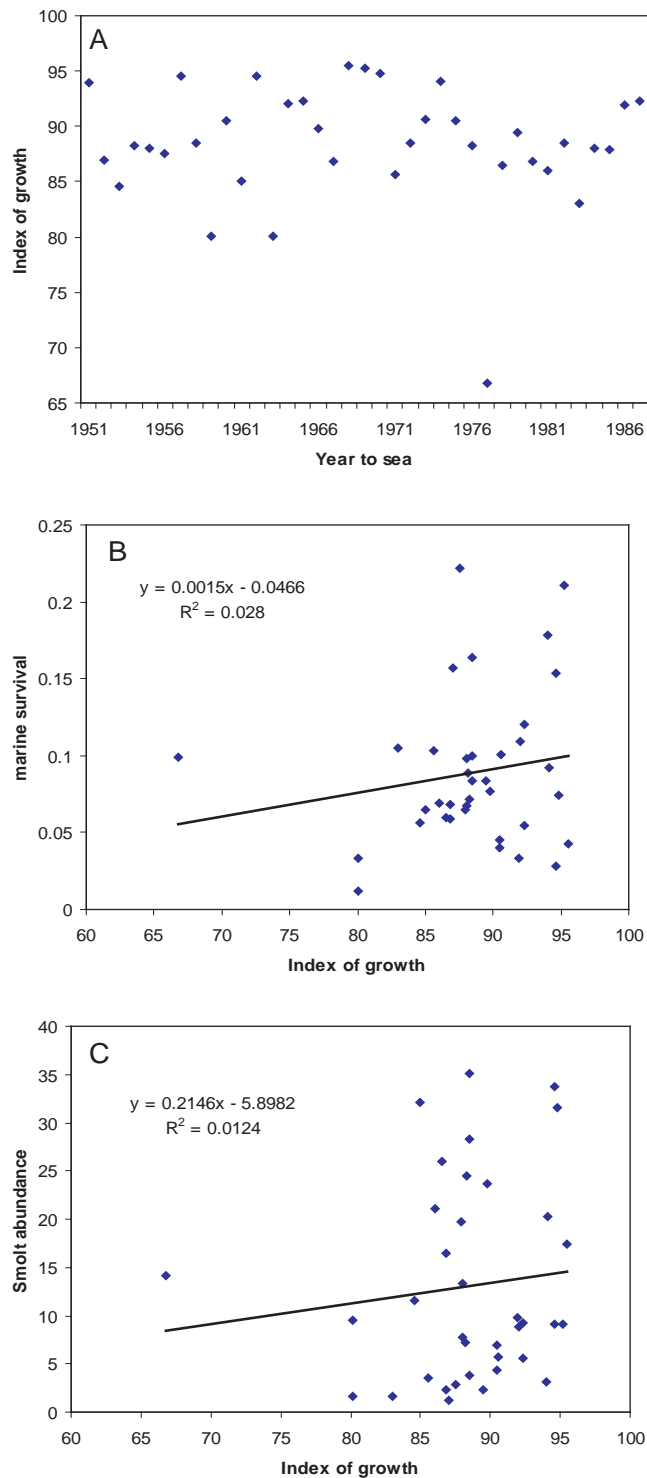
Fig. 4. Index of fish growth using scale measurements according to the methods of Henderson and Cass (1991) for sockeye salmon from Chilko Lake, British Columbia Canada. A: Index of the scale growth to the first circuli of the first marine annulus from scales removed from adult fish in fresh water. Brood year is two years earlier than the year to sea. B: The index of growth in (A) compared to the marine survival for the same brood year. C: The estimated abundance of smolts leaving Chilko Lake and the index of scale growth used in (A). Marine survival and smolt abundance data available from A. Cass (CassA@pac.dfo-mpo.gc.ca).

sented the mean scale length from the focus to the first circulus of the first marine annulus for 100 adults sampled for 37 years. The mean size of each sample was not related to the marine survival of that brood year ($R^2 = 0.028$, Fig. 4b) or to the mean size of smolts leaving the lake ($R^2 = 0.012$, Fig. 4c). The study showed that larger smolts leaving fresh water had higher survival than smaller smolts of that brood year. However, the size of adult fish at their first marine annulus was poorly related to survival. We suggest that the reason is that most of the size-related mortality had occurred prior to the first ocean annulus. The sizes in Fig. 4, as indexed by the scale measurements, are the critical sizes for this population of sockeye salmon. Large size when leaving fresh water improves survival, but it is the individuals that achieve the critical size in the ocean that make it through the first ocean winter.

These analyses provide growth after the first year at sea. If the species of salmon under investigation does not spend time growing in fresh water (i.e., pink and chum salmon), then the measurement of growth during the first year at sea provides the total size of the fish. However, examination of growth during the first summer growing season for species that spend one or more years rearing in fresh water does not provide the total size of the fish after the first summer at sea. As shown above for sockeye salmon from the Egegik and Kvichak rivers, size of juvenile sockeye salmon differs between river systems and freshwater age groups. Further, it is likely that the larger size of freshwater sockeye salmon from the Egegik River correlates to higher survival for these fish (i.e., Henderson and Cass 1991). Thus, freshwater growth may be an important component of size after the first year at sea and not including it may confound the importance of a critical size after the first summer at sea.

Evidence for Critical Period

One other test of the critical size, critical period hypothesis is that mortality after this period should be large relative to other sources of early marine mortality (Beamish et al. 2004). Estimates from the literature of marine mortality of coho, pink, and sockeye salmon at different early marine life-history stages are shown in Table 1. Estimates of early marine mortality of PWS pink salmon were not provided by Moss et al. (2005), thus, to estimate marine mortality, we used data on hatchery pink salmon releases and returns provided by the PWS Aquaculture Corporation, Cordova, AK. Our summer abundance indices of hatchery PWS pink salmon come from surveys conducted during August 2001 by the Ocean Carrying Capacity Program (Farley et al. 2001). Otoliths of pink salmon were examined to determine hatchery origin. Abundance indices for each hatchery followed the methods described in Farley et al. (2007) where the estimated survey area was 56,384 km². Information on distribution of juvenile PWS hatchery pink salmon indicated that 71% of these fish were still within PWS (Armstrong et al. 2005).

Table 1. Estimates of marine mortality during the first 40 days at sea, prior to mid-August, and after the first winter at sea for juvenile coho, pink, and sockeye salmon from various regions in the North Pacific Ocean. Catchability of 1.0 assumes every fish in front of the trawl net was caught. Catchability estimate of 0.3 for juvenile salmon is from Shuntov et al. (1993).

Catchability	Species	Region	Marine mortality		
			1st 40 days	Mid-August	Over-winter
1.0	Coho	Strait of Georgia, BC[1]			> 90%
1.0	Sockeye	Bristol Bay, Alaska[2]			66–84%
1.0	Pink	Prince William Sound Hatcheries, Alaska		> 93%	26–34%
Unknown	Pink	NE Kamchatka[3]	55–94%		55%–95%
Unknown	Pink	Bella Coola, BC[4]	55–77%		
0.3	Pink	Prince William Sound Hatcheries, Alaska		80–97%	67–78%
0.3	Sockeye	Bristol Bay, Alaska			20–30%
0.3	Coho	Strait of Georgia, BC			> 90%

[1]Beamish et al. 2004; [2]Farley et al. 2007; [3]Karpenko 1998; [4]Parker 1968.

Therefore, we appropriately expanded our estimates on the shelf to reflect those fish still in PWS.

Conservative estimates, assuming the catchability of our net is 1, for over-winter mortality of PWS hatchery pink salmon ranged from 26% to 34% (Table 1). These estimates are lower than the conservative estimates of the post-summer mortality for juvenile Bristol Bay sockeye salmon which ranged from 66% to 88% (Farley et al. 2007). Conservative estimates of over-winter mortality for PWS pink salmon were also lower than those estimated for Strait of Georgia coho salmon (> 90%) and northeast Kamchatka pink salmon (from 55% to 95%). However, if catchability were lower, (i.e. 0.3 as suggested by Shuntov et al. (1993), then estimates of mortality for PWS pink salmon increase to > 70% and are more in line with estimates for Strait of Georgia coho salmon and northeast Kamchatka pink salmon (Table 1). In either case, it is apparent that the over-winter mortality estimates for juvenile Pacific salmon from various locations in the North Pacific are substantial and indicate a need for greater understanding mechanisms that may impact growth of juvenile salmon during their first year at sea.

There is evidence that juvenile Pacific salmon in their first ocean year will use lipids for growth early in the marine period (MacFarlane and Norton 2001), but have their highest energy content later in the summer (Yerokhin and Shershneva 2000), an indication that fish store energy prior to winter. The mechanism that alters the use of lipids is not known, but it may be related to day length or it may be related to size. A critical period would be the date that would ensure that sufficient lipids were accumulated to provide energy needed during the winter. If the mechanism that changes the utilization of lipids is only partly related to size, smaller fish would not be able to compensate for their small size after the end of the critical period. Presumably, there may be a relationship with winter ocean conditions. However, in general, it may be possible to identify a time in the summer when fish of a certain minimal size have a defined probability of surviving average winter conditions.

A critical size, critical period relationship to marine survival is a reflection of the carrying capacity of an ecosystem. A recognition that insufficient growth in the first marine spring and summer probably will result in death during the winter is also recognition that there is a matching of numbers of juveniles entering the ocean with the prey that is immediately available to juvenile salmon. Natural regulation in the absence of fishing or hatcheries would result in reduced adult returns in periods of reduced prey production and large returns in periods of favourable ocean environmental conditions. In managed populations, it should be possible to use early marine growth to optimize the production of smolts entering the ocean and to forecast marine survival. Producing too many smolts during years with low ocean productivity simply results in salmon dying in the first marine winter either directly from starvation or indirectly by being easy prey.

ACKNOWLEDGMENTS

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Possible Causes and Effects of Shifts in Trends of Abundance in Pink Salmon of Kunashir Island, a Population near the Southern Limit of Its Range in Asia

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Abstract: The results of monitoring pink salmon (*Oncorhynchus gorbuscha*) spawning in the rivers of Kunashir Island are presented. The abundance of this small stock is shown to be related to its spawning location which is close to the southernmost limit of spawning for this species. Long-term changes in the number of spawners and body size are similar to those for other larger pink salmon stocks in the Sakhalin-Kuril region. These similarities suggest that factors related to habitat changes play an important role in pink salmon stock dynamics.

Keywords: pink salmon, Kunashir Island, spawning migration, abundance, body length, reproduction

INTRODUCTION

Pink salmon (*Oncorhynchus gorbuscha*), because of its unique biology (large fluctuations in abundance and the shortest life cycle of all Pacific salmon) is an attractive subject for studying stock dynamics as a process of interaction between salmon and their habitat. One way to approach such studies is to look at life cycle processes of pink salmon in different regions. In a companion paper (Kaev et al. 2007) changes in pink salmon reproduction, abundance and fork length were analyzed for the three large stocks in the Sakhalin-Kuril region, which provide more than half of the Russian pink salmon catch in the Okhotsk Sea. In this paper the pink salmon in the rivers of Kunashir Island are analyzed. The abundance of this stock is significantly less than those of the Sakhalin-Kuril stocks. However, Kunashir stock of pink salmon is interesting to researchers because their range is close to the southernmost limit of spawning for the species (Heard 1991).

MATERIALS AND METHODS

Despite the historical existence of a pink salmon fishery on Kunashir Island, regular observations of pink salmon reproduction there only began in 1994. Annual changes in reproduction indices were studied in the Ilyushin River located in the center of the island's Pacific coast (Fig. 1). The Ilyushin is a typical Kunashir river with a 9.3-km-long main stem and 21,000 m² of spawning grounds (Kaev and Strukov 1999). Each year the numbers of adult fish in the river are counted twice (in mid-September and the first half of October) at individual sites on spawning grounds. The estimate of mean density of fish (ind/m²) was multiplied by 4 (a factor we consider reasonable to account for the duration of the run and the occurrence of aggregations of fish outside the spawning grounds), and then extrapolated to obtain the total number of pink salmon that entered the river in that particular year. The numbers of pink salmon in other rivers on Kunashir were calculated based on the ratio between the size of their spawning areas and those in the Ilyushin River. In some years data were corrected if the densities of fish on spawning grounds in some rivers were significantly either greater or less than those in the Ilyushin River (Kaev and Strukov 1999). The density of pink salmon aggregations on spawning grounds is determined occasionally in the following Kunashir rivers: Tyatinka, Mostovaya, Filatov, Prozrachniy, Asin, Valentina, Pervukhin, and Severyanka (see Fig. 1). The numbers of pink salmon returns were determined as the total number of fish counted in rivers plus those caught in the commercial fishery.

Juvenile downstream migrants were counted in the Ilyushin River by the sampling method of Volovik (1967). A probable number of migrants from other rivers of the island was calculated based on the annual ratio between the number of spawners in the Ilyushin River and the number of their fry migrating downstream. Based on these data, the pink salmon survival index was calculated as the proportion of returning spawners to the total number of downstream migrants.

In the Ilyushin River, sex, stage of maturity, fork length, body weight, and fecundity were measured in fish sampled
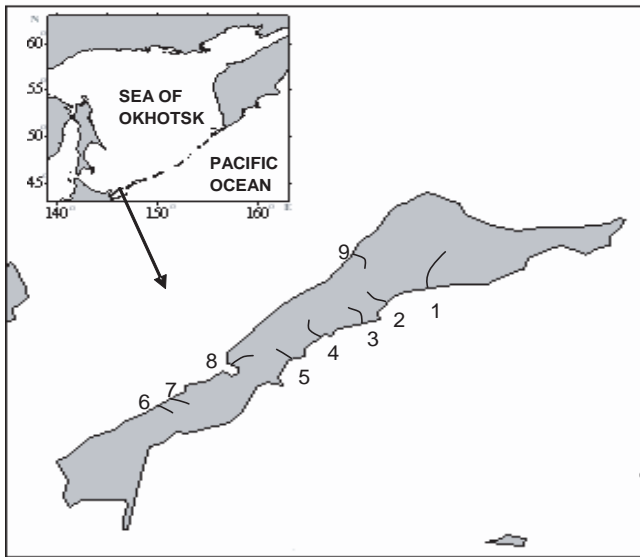
Fig. 1. Map of Kunashir Island and the location of rivers mentioned in the text. 1, Tyatinka R.; 2, Mostovaya R.; 3, Filatov R.; 4, Ilyushin R.; 5, Prozrachniy R.; 6, Asin R.; 7, Valentina R.; 8, Pervukhin R.; 9, Severyanka R.

at the river mouth with beach seines. During the observation period, a total of 55 samples (4,089 fish) were collected in 1991–2004; additionally, three samples (300 fish) were collected in 2003–2004 from trap nets in the sea. Previously, the mean indices from samples collected during a year were used for determining pink salmon biological characteristics (Kaev and Romasenko 2003). In this paper, in order to study long-term changes in pink salmon biological indices, we used the weighted average values for each index in accor-

dance with the dynamics of commercial catches. To study the timing of fish approaches to the coast, we used data only from trap-net catches (passive fishing gear). Differences in dates of approach for the different year-classes of pink salmon were estimated by the dates when half of the fish were caught.

Standard methods were used for statistical analysis (Plokhinsky 1970). Trend lines were calculated by 4-year moving averages because the inter-annual changes in pink salmon abundance and biological indices are related to its two-year life cycle.

The following symbols are used in the text: *M* (mean), *SD* (standard deviation), *CV* (coefficient of variation), *Lim* (range), *R* (coefficient of correlation), *P* (level of probability), and *N* (sample size).

RESULTS

Kunashir is the southernmost island in the Large Kuril Ridge (Fig. 1). The climate there is relatively mild, but with snowy winters with frequent thaws, as is common for the southern Large Kuril Ridge. The coastal temperature regime is influenced by the warm waters of the Soya Current. Kunashir Island is located in a relatively "warm" zone compared to nearby Iturup Island (Brodsky 1959; Kusakin 1971) where the pink salmon reproduce very successfully (Kaev et al. 2006).

The mean annual pink salmon catch in Kunashir Island waters was 3,539 tons in 1994–2004. This value reflects a stock level that increased dramatically in the 1990s following a long period of decline (Fig. 2). Based on the synchronous changes ($R = 0.92$; $P < 0.001$; $N = 15$) in commercial catches
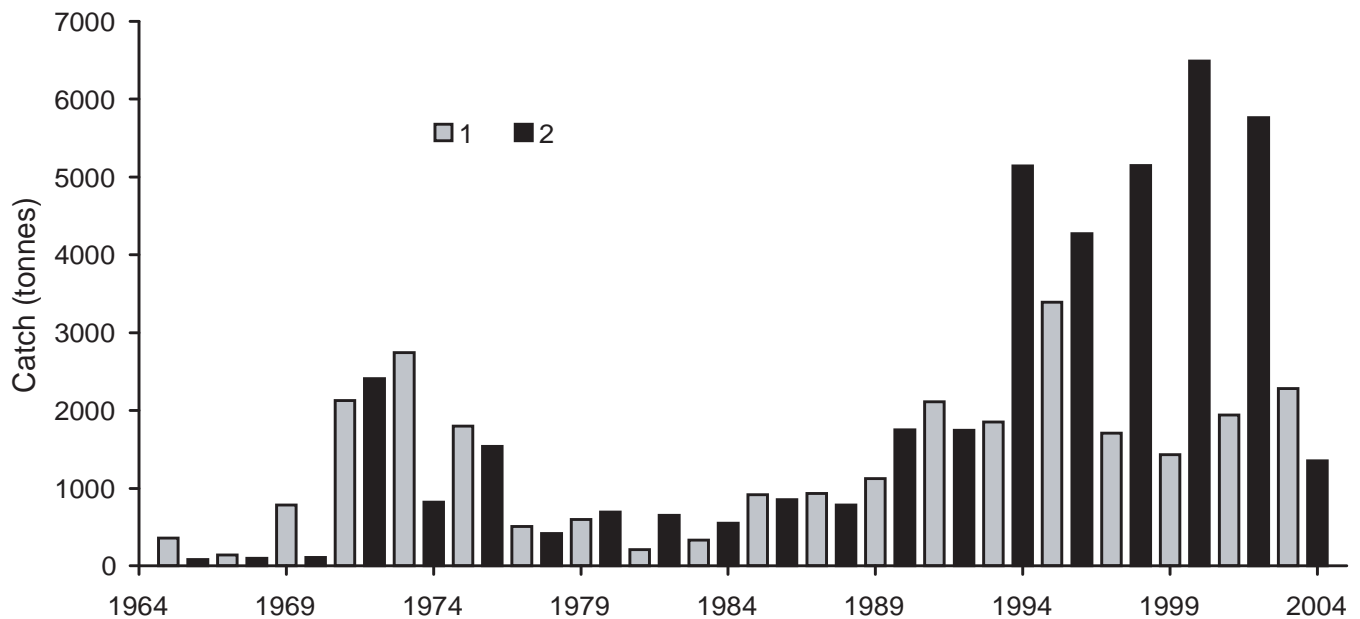

Fig. 2. Dynamics of pink salmon commercial catches in odd (1) and even (2) years on Kunashir Island from 1965–2004.

Table 1. Ratio between the numbers of pink salmon entering the rivers of Kunashir Island, the numbers of fry migrating downstream and the numbers of adult returns. Numbers of fish are given in thousands of individuals.

| Spawning | | Number of fry migrants | Adult returns | | |
Year	Fish entering rivers		Comm. fishery	Fish entering rivers	Total (SI*, %)
1989	—	55,477	1,376	1,647	3,023 (5.45)
1990	1,115	67,598	1,177	1,216	2,393 (3.54)
1991	1,647	160,794	1,022	988	2,010 (1.25)
1992	1,216	—	4,186	2,153	6,339
1993	988	—	2,019	1,026	3,045
1994	2,153	123,518	3,164	1,743	4,907 (3.97)
1995	1,026	84,317	1,007	830	1,837 (2.18)
1996	1,743	220,729	4,051	2,622	6,673 (3.02)
1997	830	37,367	859	596	1,455 (3.89)
1998	2,622	99,837	4,062	2,888	6,950 (6.96)
1999	596	67,480	1,154	469	1,623 (2.41)
2000	2,888	271,735	3,409	2,613	6,022 (2.22)
2001	469	22,243	1,427	671	2,098 (9.43)
2002	2,613	187,277	816	426	1,242 (0.66)

*SI, survival index.

and the number of fish in rivers (Table 1), the fishery is based on a single (local) stock. The stock reproduces in 40 rivers and brooks, and the inlets to 5 lakes. The total spawning area of the local pink salmon stock is approximately 266,000 m². The island's rivers are relatively short. In most rivers, aggregations of pink salmon spawn at sites several kilometers upstream from the mouth. From 426 to 2,888 (average 1,400 thousand fish) entered Kunashir rivers in 1990–2004. From 22,243 to 271,735 (average 116,531 thousand) fry migrated downstream in 1990–1992 and 1995–2003. Pink salmon returns in 1991–2004 ranged from 1,242 to 6,950 (average 3,544 thousand individuals), of which 816 to 4,062 (average 2,124) thousand fish were caught in the commercial fishery. On the average, during 1991–2004 the number of pink salmon in even years (4,932 thousand fish, $CV = 42.2\%$) was higher than in odd years (2,156 thousand fish, $CV = 27.4\%$).

Despite the odd-year/even-year changes in pink salmon numbers, the mean number, based on the trend lines, changed insignificantly during the observation period (Fig. 3A). When pink salmon numbers in the even years (1992, 2004) were lower than in the following odd year, a decline in the mean stock level was observed. After the abrupt shift in the dates of run in 1993, they changed insignificantly in the following odd year. At the same time, earlier fish returns were observed in even years resulting in a consistent decrease in the trend line (Fig. 3B). After a slight decrease in the second half of the 1990s, a trend toward an increase in pink salmon fork length was seen (Fig. 3C). In most years there was an inverse relationship between pink salmon numbers and fork length. The correlation between fish numbers and dates of

run was weak and differed by sign ($R = 0.44$; $P > 0.05$) and trend lines ($R = -0.32$; $P > 0.05$). The correlation between fish numbers and fork length was more significant, when we analyzed the actual measured values ($R = -0.68$; $P < 0.01$), than the trend lines ($R = -0.56$; $P < 0.05$). A relation among the biological indices measured is closer than the calculated values in the trend lines. This may be a result of changes in contiguous years. To study this problem (see Kaev et al. 2007), we combined the data on pink salmon numbers, dates of run, and fork length into groups. In the first group the number increased compared to those of the previous year. In the second group the number declined. In the third group the number did not change. Changes in the timing of the spawning run and fork length in contiguous years were considered within each group. The designation 'without change' was applied if a change did not exceed the statistical error of the mean of the sample being examined. Data from two groups of pink salmon were analyzed: (1) abundance of fish from Kunashir Island; and (2) abundance of fish from the broader region, encompassing eastern Sakhalin Island, the southern Kuril Islands and Hokkaido. For Kunashir pink salmon changes in dates of run and fork length were shown to coincide with the corresponding changes in abundance in most cases (Table 2). In 12 of 13 cases with an increase (or decrease) in numbers, the dates of run were shifted toward later (or earlier) dates ($R = 0.77$; $P < 0.01$; $N = 13$). Changes in the fork length also varied synchronously with the abundance numbers in 10 of 13 cases, but these changes were opposite in direction ($R = -0.69$; $P < 0.01$; $N = 13$). When we used the data on abundance of fish from the broader region,
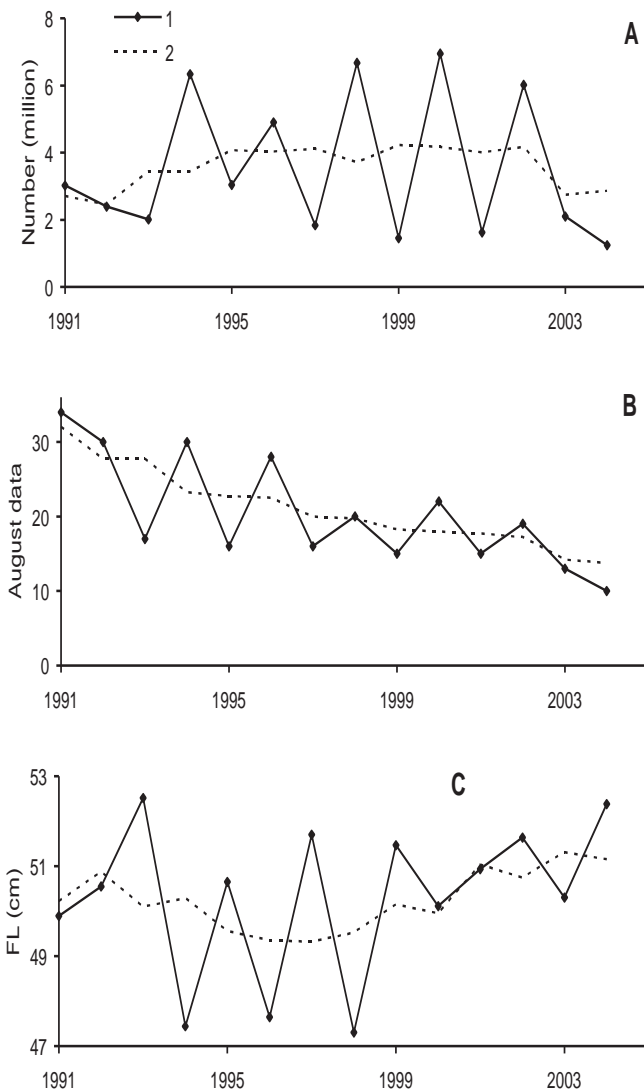
Fig. 3. Changes in numbers (A), date of 50% capture (B) and fork length (C) of pink salmon from Kunashir Island from 1991–2004. 1, measured values; 2, trend lines.

there was no clear pattern regarding either changes in dates of run ($R = 0.22$) or fork length ($R = -0.38$).

A close relation between the number of spawners entering rivers and the number of the subsequent downstream migrating fry was established (Fig. 4A). Taking into account the almost seven-fold fluctuation in the number of spawners on the spawning grounds in different years, this dependence becomes the essential factor in determining the number of offspring. However, a dependence of the number of offspring on the number of their parents numbers weakens significantly at the final stage of the reproductive process (actual returns) (Fig. 4B), because different pink salmon year-classes have different levels of survival during the marine period (Fig. 5A). In particular, an increase in pink salmon mortality during the marine period has been shown for year-classes with high numbers of downstream migrating fry (Fig. 5B).

DISCUSSION

The pink salmon of Kunashir Island have some unique biological characteristics that distinguish them from other pink salmon stocks in the Sakhalin-Kuril region (Kaev et al. 2007). First, during spawning in the Kunashir rivers a close relationship is seen between the number of spawners and the subsequent number of downstream migrating fry. This pattern is uncommon in fish from similar small rivers in other reproductive areas. Second, a clear decrease in fish survival during the marine period is seen in Kunashir pink salmon year-classes with high numbers of downstream migrating fry. Third, Kunashir pink salmon returns from abundant year-classes were typically smaller in length and approached the coast at later dates, in accordance with the principles of density regulation. The question arises whether these differences in Kunashir pink salmon occur because of interaction(s) with their habitat or for other reasons. While searching for the answer to this question, we noted the comparatively low density of spawners on the spawning grounds of the Kunashir rivers. Since 1994 through 2004 the mean

Table 2. Co-dependence of changes in dates of run and fork length (FL) with species abundance in pink salmon from Kunashir Island (Kunashir) and in the broader region* (Region) in contiguous years.

Changes in indices		Kunashir		Region	
Abundance	Dates of run and fork length	Dates of run	FL	Dates of run	FL
Increase or decrease	Synchronous with abundance	12	2	5	5
	Asynchronous with abundance	0	10	7	7
	Without change	0	0	0	0
Without changes	With change	1	1	1	1
	Without change	0	0	0	0

*The eastern coast of Sakhalin, and the southern Kuril and Hokkaido islands (Anonymous 2004).

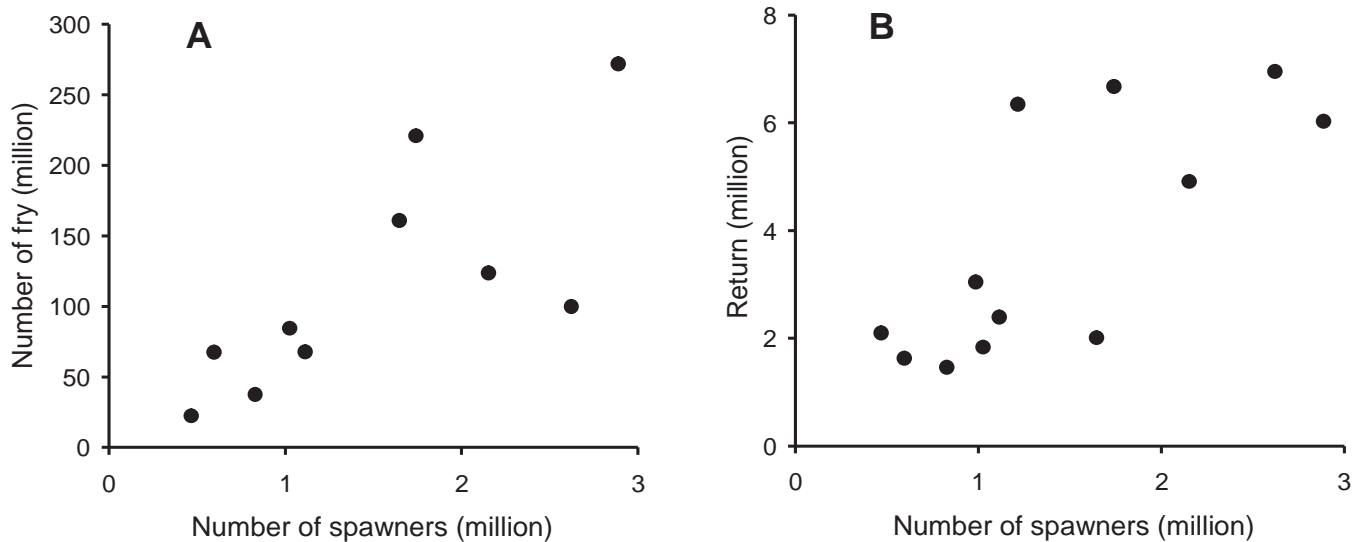322

Fig. 4. Dependence of numbers of pink salmon fry migrants (A) (R = 0.78; P < 0.01; N = 12) and returns (B) (R = 0.53; P > 0.05; N = 13) on the number of spawners in Kunashir Island rivers from 1990–2004.
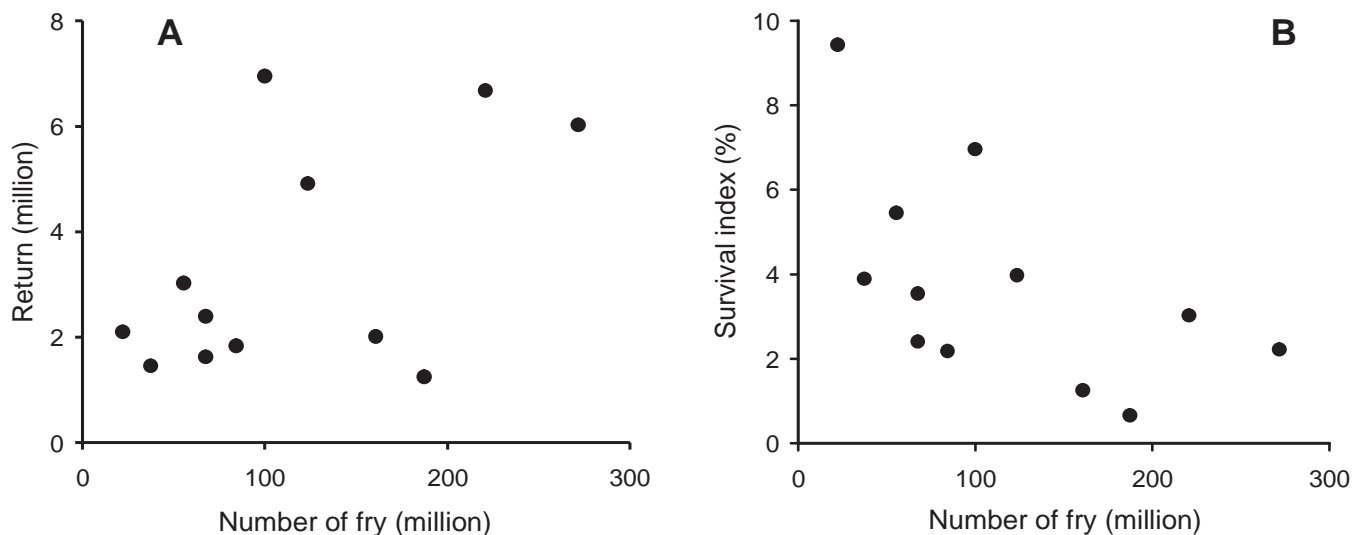

Fig. 5. Dependence of pink salmon returns (A) (R = 0.52; P > 0.05; N = 12) and fish survival during the marine period (B) (R = -0.57; P < 0.05; N = 12) on the harvest of fry migrants in Kunashir Island rivers from 1990–2004.

pink salmon concentration on the Kunashir spawning grounds during the peak of spawning (mid-September) was 1.35 ind/m². while on neighboring Iturup Island the level was 2.11 ind/m². Also, the number of spawners in Kunashir rivers in different years varied significantly (CV = 59.4, a 6.8-fold difference between extreme values) compared to Iturup rivers (CV = 27.1, a 2.9-fold difference). We also note that the only region of the three areas considered by Kaev et al. (2007) where a consistent positive relation was observed between the number of downstream migrating fry and the number of their parents, is the Aniva Bay coast. The mean concentration of spawners there was 1.56 ind/m² during the peak of spawning. Thus, we suggest that the increase in numbers of

fry migrants, observed simultaneously with an increase in the number of spawners in the Kunashir rivers, is related to the complete use of the spawning grounds.

Based on occasional observations, juvenile pink and chum (*O. keta*) salmon remain in the shallow water at the coast of Kunashir Island after they migrate downstream, as they do on Iturup Island (Kaev and Chupakhin 2002). These observations are documented by the rare occurrence of juveniles in purse-seine catches and in trawls in June and July close to the island shores (Kaev et al. 1994; Kovalenko et al. 2004; Shubin et al. 2005). We have no reason to think that the survival of Kunashir pink salmon in the open ocean differs significantly from that of pink salmon stocks in surrounding

areas. The increase in mortality for year-classes with high numbers of fry migrants, occurs in the early marine period that is characterized by the highest and most variable rate of pink salmon mortality (Heard 1991; Karpenko 1998). A comparatively slow rate of growth (determined by examination of scales) during the early marine period is common for Kunashir chum (Kaev 1998) and pink salmon (Kaev and Romasenko 2001). Therefore, the increase in pink salmon mortality in year-classes with very abundant fry migrants (Fig. 5B) can be attributed to density-dependent factors. In this vein, we should note that the level of Kunashir pink salmon survival during the marine period (the mean survival index is 3.75%) is lower and its variability higher ($SD = 2.66$) than the corresponding indices in the same years of observations in the pink salmon of Iturup Island ($M = 5.32$; $SD = 1.81$), and the southeastern coast ($M = 5.71$; $SD = 2.49$) and Aniva Bay ($M = 4.66$; $SD = 2.49$) on Sakhalin Island.

As in other areas of the Sakhalin-Kuril region (Kaev et al. 2007), the differences in size composition and the timing of the pink salmon run on Kunashir Island are related to the dates when early- and late-spawning groups enter the rivers (Kaev, 2002). From 15 through 25 August the early-spawning group is replaced by the late-spawning group. We know this because of the presence of large males in catches (Fig. 6). Following the abrupt decline in numbers of the late-spawning group in 1993, during 1994–2003 the odd year-classes became significantly less abundant than the even year-classes. Because the early-spawning group was more abundant during odd years from 1994–2003, the approach to the coast in odd years ended earlier than in even years, suggesting a clear relationship between the inter-annual changes in Kunashir pink salmon numbers and dates of run (Fig. 3). However, in recent years a gradual decline in dates of approach of late-spawning fish was also seen in even year-classes (Fig. 6), producing a decline in the pink salmon stock in 2004 (Fig. 2). The two-year cycle in changes of pink salmon body length, shown in the 1990s, has also been
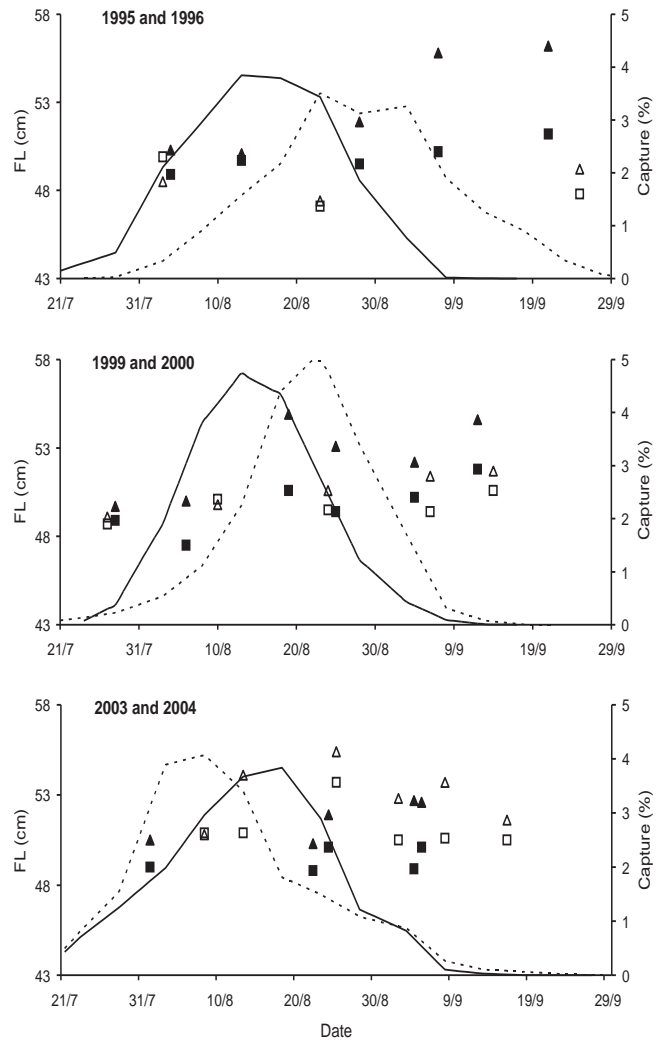
Fig. 6. Dynamics of catches and changes in pink salmon fork length on Kunashir Island in 1995–1996, 1999–2000, and 2003–2004. Lines indicate daily catches in odd (solid line) and even (dotted line) years; symbols indicate male (triangle) and female (square) fork lengths in odd (dark symbols) and even (light symbols) years.
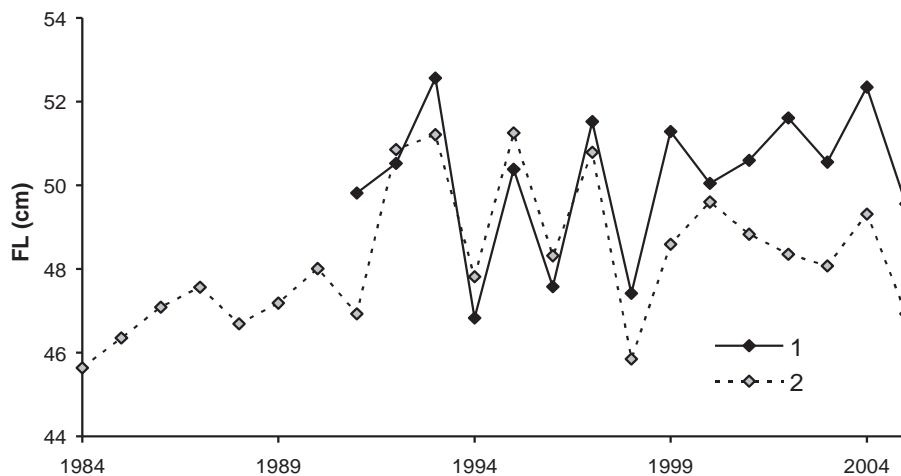

Fig. 7. Changes in fork length of pink salmon from Kunashir (1) and Iturup (2) (from Kaev et al. 2006) islands in 1984-2005.

broken in recent years (Fig. 3).

Changes in abundance and biological indices of pink salmon on Kunashir Island have been studied for only a comparatively short period of time, beginning in the 1990s. During these years, changes in commercial catches correlated ($R = 0.97$; $P < 0.001$; $N = 14$) with changes in the total abundance of pink salmon (fish caught, plus fish entering the rivers). Thus, we suggest that the increase in pink salmon catches on Kunashir Island since the 1990s (Fig. 2) is related to the increase in stock abundance, not to other causes (for example, an increase in catch rate). Since the 1990s, the fork lengths of Kunashir pink salmon (Kaev and Romasenko 2003) were close to those of the Iturup pink salmon (Kaev and Chupakhin 2003) and larger than the fork lengths of the southern Sakhalin pink salmon (Kaev et al. 2004). The interannual changes in the fork lengths of Kunashir pink salmon were similar to those of pink salmon on Iturup Island (Fig. 7) where the abundance of pink salmon was also higher in even years during the period of investigation. Thus, we suggest that large sizes of fish corresponded to periods of large catches of pink salmon on Kunashir Island as well as on Iturup Island and southern Sakhalin Island (Kaev et al. 2007). However, changes in the fork length of Kunashir pink salmon, occurring together with changes in abundance, can be explained by a density-dependent concept. These changes could be considered as a special case, because the pink salmon on Kunashir Island, unlike in other areas (Kaev et al. 2007), have been studied for a comparatively short period of time. In addition, the relationship between abundance and fork length revealed for the Kunashir pink salmon becomes weaker on a larger scale, when instead of this small stock of Kunashir Island we use the abundance of the regional pink salmon stock (Table 2). A shift in the timing of fish approaches to the coast toward earlier dates is also not unique to Kunashir pink salmon. In other areas similar trends have been seen since the mid 1990s (Kaev et al. 2007).

At the same time, the Kunashir pink salmon have some features that distinguish them from fish from other Sakhalin-Kuril areas. First, the number of fry migrants increases with an increase in number of spawners which is not common for such small rivers. This feature is caused by an incomplete use of spawning grounds in rivers that is attributed to low stock abundance. Second, there is a clear decline in fish survival during the marine period for year-classes with abundant fry migrants; this may be caused by a lack of resources during the early marine period for very abundant year-classes of fry. We suggest that these observations reflect specific habitat requirements of pink salmon near the limit of the spawning habitat for this species.

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Similarity of Diurnal Rhythms of Pacific Salmon Feeding in the Western Bering Sea

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Abstract: Research on diurnal rhythms of salmon feeding is important for calculations of daily diets and evaluation of food sufficiency. The acquisition of such information requires datasets from trawling conducted during both day and night. The TINRO-Centre survey by RV *TINRO* in the western Bering Sea during the autumn of 2004 allowed for such data acquisition. Based on data averaged for several biostatistical areas, it was shown that small immature individuals (< 30 cm in fork length) of five Pacific salmon species had similar diurnal feeding patterns. They fed most intensively between 11:00 a.m. and dusk. Food was digested relatively quickly, and stomachs were essentially empty by 6:00 to 7:00 a.m. Older immature and maturing individuals had diurnal patterns that are less clear. This is probably related to food composition, and weak relationships between forage activity, time of day, and the time required to digest larger food items. If the degree of digestion is well defined, it is possible to define diurnal feeding patterns in some cases. When Hyperiidae are the primary food item, it is not possible to define the time of food intake precisely, because their chitinous shells hamper quick digestion.

Keywords: daily rhythms, salmon, feeding, diet, nekton, zooplankton

INTRODUCTION

One of the main challenges of marine nekton trophic ecology is defining the 24-hour food ration of organisms, especially fish. This is needed for practical calculations as well as for compiling total ecosystem balance equations. There are two ways of detecting the 24-hour food ration: experimental (in aquaria) or by measuring diets in the natural environment.

Natural observations are both preferable and possible using trawling surveys. In order to estimate the 24-hour food ration, however, it is necessary to estimate daily feeding rhythms, variability in food composition over 24 hours, and the speed of digestion. For these reasons, TINRO-Centre has developed a method (Chuchukalo and Volkov 1986) that has been used for several years in applied research. Depending on the particular objective, the daily feeding rhythms can be defined through measuring the daily dynamics of: a) stomach fullness, b) the presence of fresh or partially digested food, and c) the presence of empty or nearly empty stomachs (Volkov 1994; Volkov et al. 1997).

To study daily feeding patterns, the ideal approach would be to conduct frequent trawling surveys on several days at one location. However, in practice, during large-scale complex surveys this is not always possible. During one or several days a large number of fish stocks and dispersed individuals pass through a sampling area at a high rate of speed, which is typical for salmon. That is why, during the occupation of each station, the samples collected may not be representative of feeding at a particular site. This is why the observations from our trawls are combined, and a "synthetic" daily station is created with sufficient samples to arrange them into 1–2 hour intervals. This paper reports the results of a study of the 24-hour feeding patterns in pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), coho (*O. kisutch*) and chinook (*O. tshawytscha*) salmon in the Russian Far Eastern seas.

MATERIALS AND METHODS

The basic method to detect 24-hour feeding rhythms is research on the dynamics of stomach fullness, i.e. the fullness indices that in Russian trophic ecology are traditionally expressed in parts per ten thousand ($^o/_{ooo}$). Studies on chum salmon feeding in the western Bering Sea which are based on the presence of fresh food, clearly show a single midday peak, using the 5-point system for identification of the level of food digestion (Fig. 1): 0 - fresh food, 1 - digestion hardly appreciable; loss of transparency, 2 - skin and muscles noticeably damaged, 3 - semi-digested fragments present, and 4 - digested matter present. However, in this example the dominant food item was *Clione limacine*. Its freshness in the stomach is reliably detected visually. One can also detect the freshness of recently eaten copepods and euphausiids,

which are transparent in the plankton, but in stomachs they quickly turn opaque. However, if the food is hyperiid amphipods, a very common prey for salmon, it is difficult to determine their freshness visually, because their chitinous shells hamper quick digestion. That is why the presence of these species may result in a more complicated pattern than that shown in Fig. 1 (Volkov et al. 1997).

For the analysis of the diurnal feeding rhythms of salmon, samples were collected during surveys for the TINRO-Centre aboard the RV *TINRO*. Materials were collected from 11 September to 23 October 2004 in a deepwater zone of the western Bering Sea and western North Pacific Ocean (Table
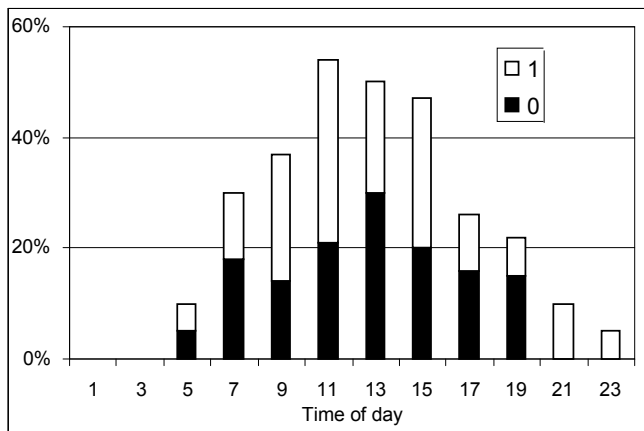
1, Fig. 2).

The charts with daily feeding patterns of salmon are based on data collected from trawls (Table 1). For tests on the feeding of nekton we sampled 25 stomachs of each size class, and for salmon 10 stomachs were sampled. Smaller samples of salmon were necessary as they often were in abundance.

RESULTS AND DISCUSSION

The daily rhythms of feeding intensity of immature salmon (30 cm or less in fork length) for all five species had much in common (Figs. 3–7). At daybreak most stomachs were empty or nearly empty. After sunrise, feeding activity rose rapidly, stomach fullness increased, and by mid-day it reached its first maximum. Then the digestion process exceeded food consumption, as evidenced by the decline in stomach fullness. By the end of the day feeding activity rose again, and during the period from twilight to early darkness stomach fullness reached its second maximum, which was usually greater than the first. Stomach fullness then declined as food was digested during the night, although some fish might continue feeding.

We note that salmon feed predominantly during daylight. As a result, their consumption of plankton should be calculated based on catches in the upper 50-meter layer (Volkov 1994) to estimate the daylight food base. The results of tagging programs using archival tags show that salmon are able to live and feed throughout a wide range of depths (down to 200 m) and temperatures, but the main feeding area is in the upper pelagic (i.e. water layer not deeper than 50 m). In order to make a quantitative estimation of the salmon food

Fig. 1. Diurnal rhythms of chum salmon (50–70 cm in fork length) in the Bering Sea in summer. 0 = fresh food (solid); 1 = digestion hardly appreciable, loss of transparency (open); Y axis = % fullness (after Volkov 1994).
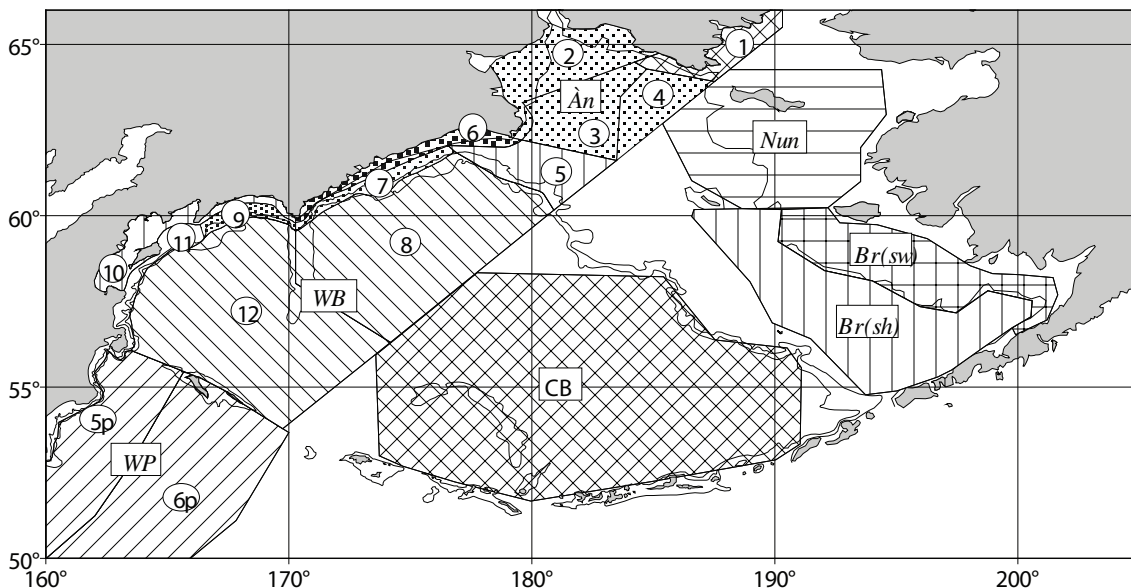

Fig. 2. Biostatistical areas of the Bering Sea and western North Pacific Ocean. WP = western North Pacific Ocean; WB = western Bering Sea; CB = central Bering Sea; An = Anadyr Bay; Nun = Nunivak; Br = Bristol Bay. Samples were collected in areas 8 (WB), 12 (WB), 5p (WP), and 6p (WP).

Table 1. Fork length categories of fish and number of trawls and stomach samples on which Figs. 3-7 are based.

	Pink		Chum		Sockeye			Coho		Chinook	
Fork length (cm)	15-20	20-30	15-20	30-40	15-25	30-40	40-50	20-30	30-40	20-30	40-50
Number of trawls	15	17	20	17	17	10	20	20	10	9	10
Number of samples	214	258	160	263	93	146	119	65	33	15	19
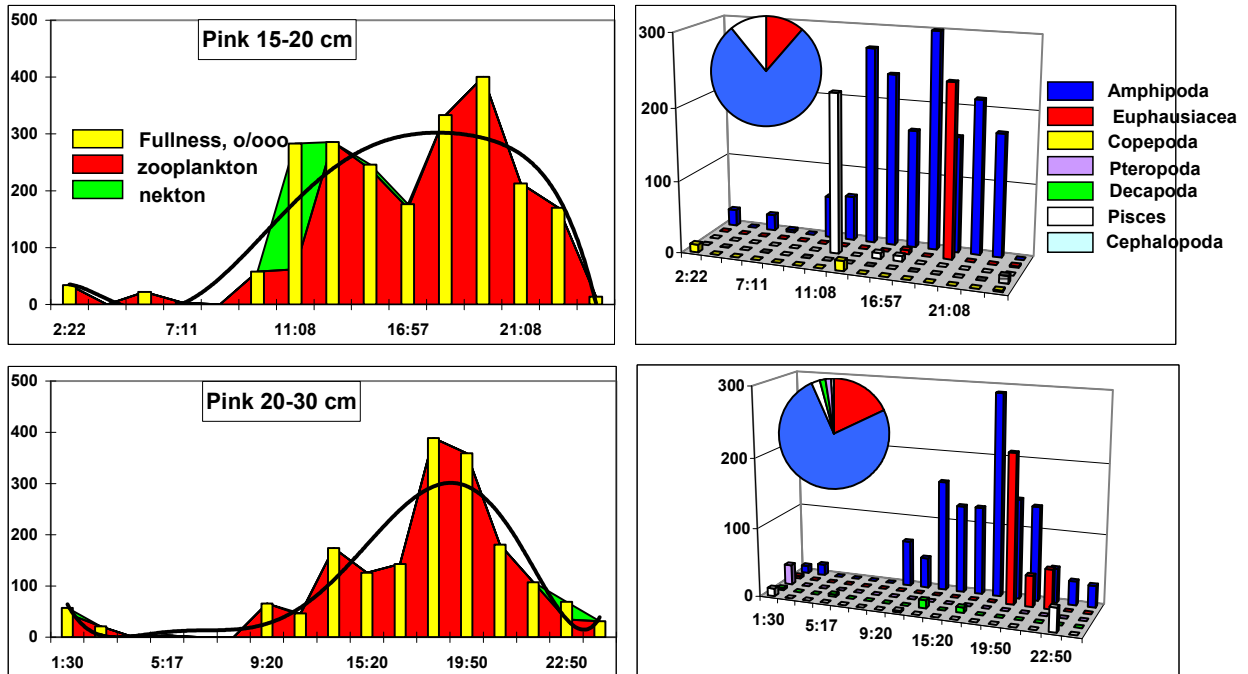
Fig. 3. Diurnal rhythms of pink salmon feeding in the Bering Sea during the autumn of 2004. Left-hand panels: stomach fullness ($^o/_{ooo}$), structure of plankton and nekton. Right-hand panels: taxonomic composition of foods. Circular diagram = daily average structure of foods. X axis = time of day; Y axis = $^o/_{ooo}$.

Fig. 4. Diurnal rhythms of chum salmon in the Bering Sea during the autumn of 2004. Legend as in Fig. 3.

Fig. 5. Diurnal rhythms of sockeye salmon feeding in the Bering Sea during the autumn of 2004. Legend as in Fig. 3.

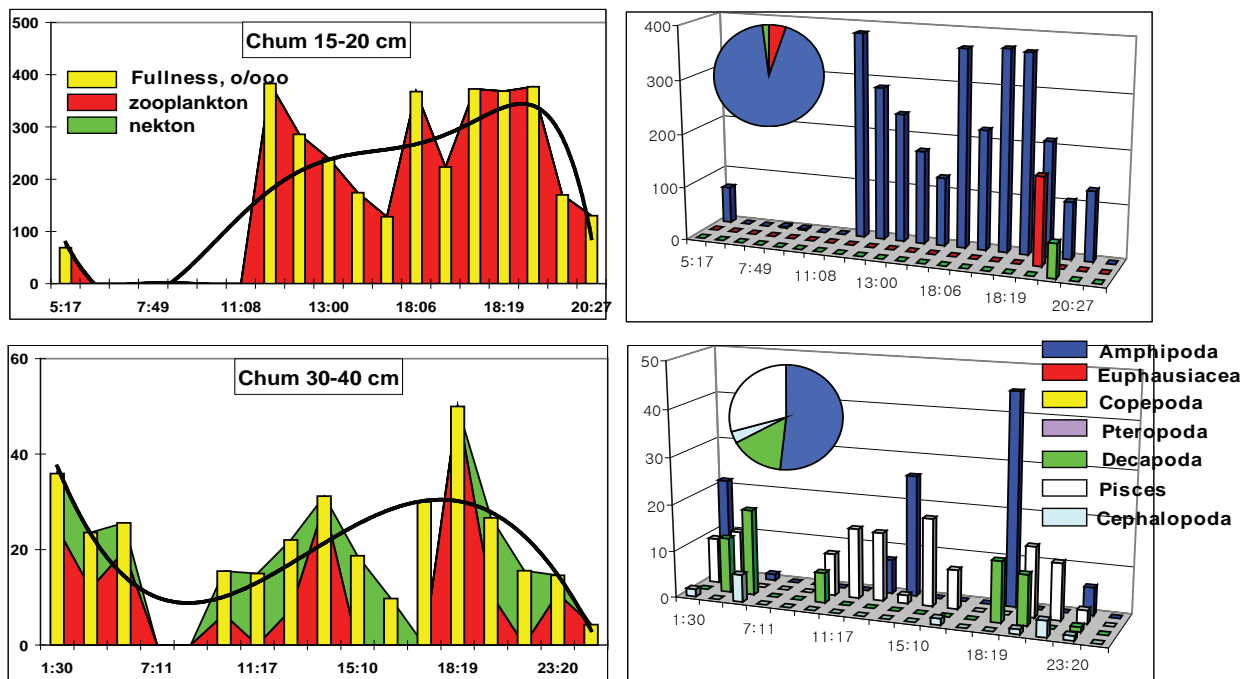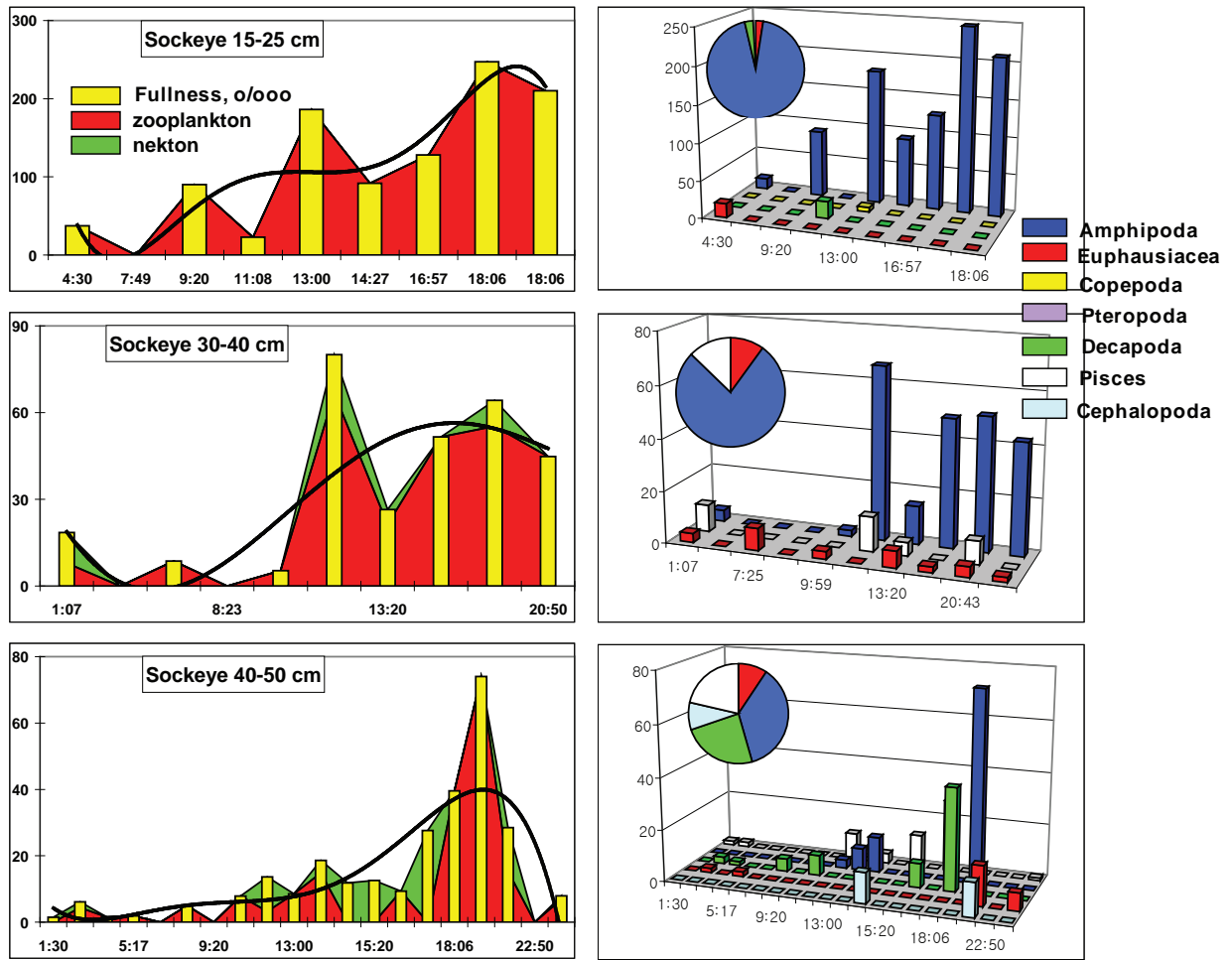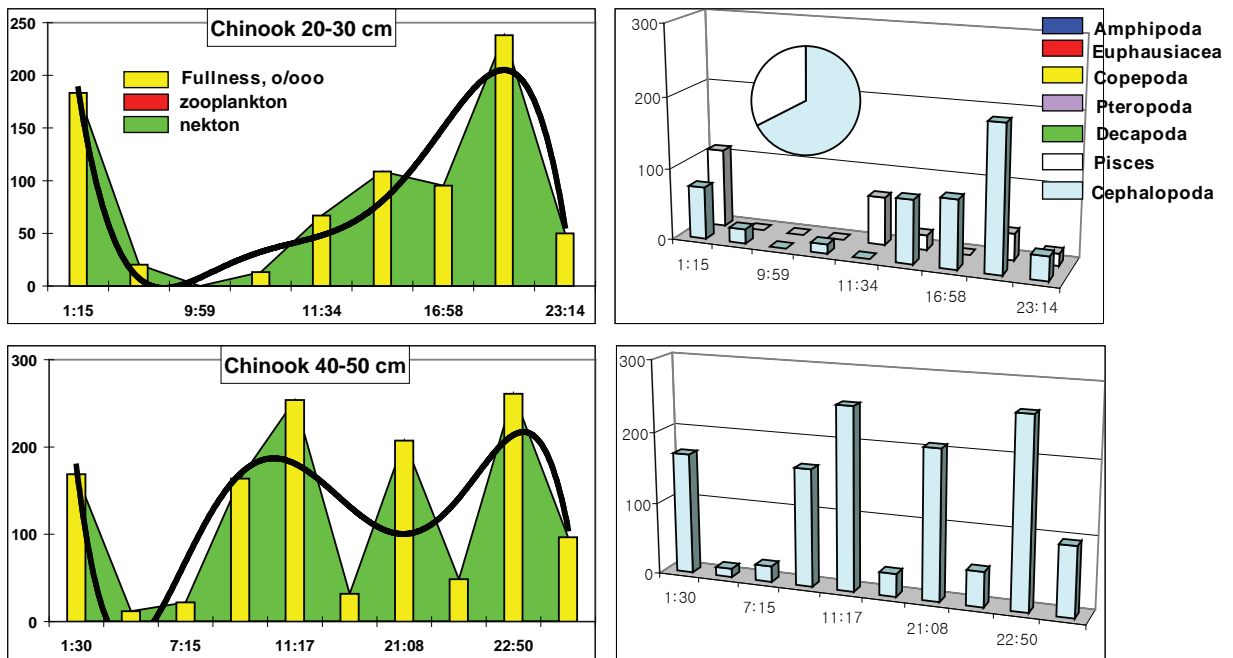**Fig. 6.** Diurnal rhythms of coho salmon feeding in the Bering Sea during the autumn of 2004. Legend as in Fig. 3.
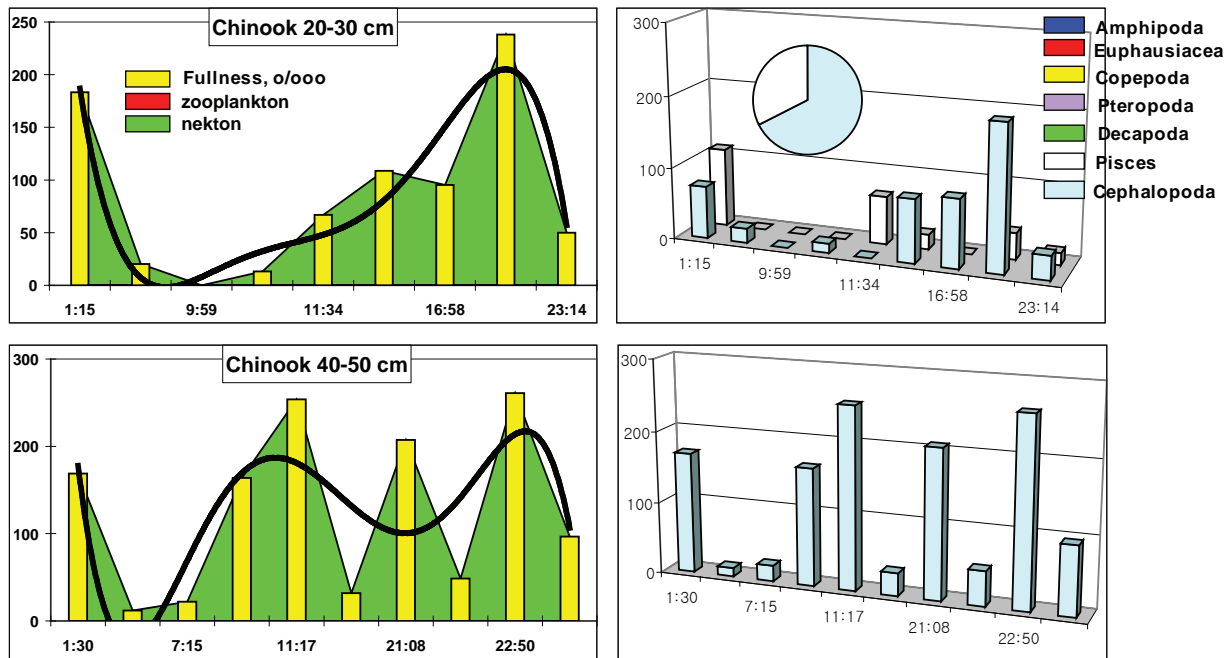
Fig. 7. Diurnal rhythms of chinook salmon feeding in the Bering Sea during the autumn of 2004. Legend as in Fig. 3.

base, it is necessary to take into consideration the type and time of feeding, and the selectivity for certain plankton types that constitute the food base.

We observed that the stomach fullness of salmon is lowest at daybreak. This is also typical for salmon in the eastern Bering Sea (Ueno et al. 1969; Godin 1981; Davis et al. 2000; Schabetsberger et al. 2003), as well as for underyearling and young salmon in the Okhotsk Sea (Shimazaki and Mishima 1969; Gorbatenko and Chuchukalo 1989; Volkov 1996a, b; Volkov et al. 1997; Lazhentsev and Bokhan 2001). Considering that salmon feed predominantly during the day, they should be regarded as optical or visual predators, although in some regions feeding also takes place at night. Birman (2004) has written that in certain cases visual receptors are not the only means by which salmon find food at night. However, many prey species consumed by salmon at night have luminous organs (euphausiids, squids, myctophids, e.g.). Because the type of luminescence (the number of photophores) is specific for each prey, this suggests that at night, salmon may be able to distinguish among different types of prey.

Plankton vertical catches indicated that the proportion of hyperiids in the plankton was relatively small compared to that of copepods, chaetognaths and euphausiids (Tables 2 and 3). The most common food for pink, sockeye, and chum salmon was hyperiids (e.g. see circular diagrams on the right-hand side of Figs. 3–5), and specifically *Themisto pacifica*. One explanation may be that because *T. pacifica* form very tight agglomerations on the water surface (Chebanov 1965), it becomes an easy prey for daytime predators. Salmon also preferred pteropods (Volkov 1994; Volkov et al. 1996b;

Volkov et al. 1997). However, the biomass and quantity of pteropods throughout the season and years are subject to sharp changes. Further, their share in the salmon forage base also varies a great deal. For example, in 2004 the proportion of pteropods in the plankton samples and in the chum salmon diet was insignificant, but in 1992 they clearly dominated, reaching more than 50% (Volkov 1994).

The proportion of euphausiids in the salmon diet can also be great (Volkov 1994; Volkov et al. 1997), however it depends on their abundance in the plankton, on the presence of other food sources (hyperiids and pteropods), and on the time of day. Thus, during our studies in autumn 2004 in deepwater regions, the biomass of euphasiids during the day in the 0–50 m layer did not exceed 6 mg/m^3, although in the 50–200 m layer it was greater. At night, however, the number was one or two orders of magnitude higher (Table 2). This is why pink and chum salmon preyed most heavily on euphausiids at twilight, when euphausiids moved toward the surface (Figs. 3 and 4). The food base for coho and chinook was nekton, fish and squid, however, for coho, there was also a large proportion of zooplankton, particularly hyperiids and euphausiids (Figs. 6 and 7).

Investigation of the diurnal feeding habits of juvenile Pacific salmon (pink, chum, sockeye, coho, and chinook salmon) over 24 hours conducted in the western Bering Sea and adjacent waters has revealed the uniformity of their feeding rhythms regardless of whether nekton or zooplankton were the dominant components in the food. These salmon species, being visual predators, consume food predominantly during the daytime. At night they digest the food, with the food generally being totally digested by dawn. Taking into

Table 2. Zooplankton biomass (mg/m³) of the large fraction in the western North Pacific Ocean (WP) and Bering Sea (WB) during day (d) and night (n). Sampling areas are indicated in Fig. 2.

| Zooplankton | Layer (m) | Biomass (mg/m³) | | | | | | | |
| | | 5p (WP) | | 6p (WP) | | 8 (WB) | | 12 (WB) | |
		d	n	d	n	d	n	d	n
Copepoda	0-50	119.4	233.6	148.7	290.8	43.7	34.9	64.6	102.1
	50-200	89.1	72.5	102.0	77.5	32.7	46.5	68.7	29.0
Euphausiacea	0-50	5.4	51.3	2.1	168.7	3.0	151.6	0.4	150.1
	50-200	5.5	32.1	6.4	168.1	76.3	147.1	16.7	101.8
Amphipoda	0-50	8.2	41.5	6.9	32.9	9.8	7.9	10.2	26.5
	50-200	4.9	21.1	13.5	19.2	9.0	15.3	5.8	6.1
Pteropoda	0-50	0.2	0.8	1.1	0.5	0.1	0.0	0.0	0.0
	50-200	0.3	1.3	0.1	0.3	0.3	0.3	0.3	2.1
Sagitta	0-50	167.9	224.5	114.2	254.3	305.4	206.5	234.0	376.3
	50-200	136.4	46.4	110.8	77.1	55.7	102.4	152.6	85.0
Coelenterata	0-50	1.6	30.4	1.1	17.2	3.6	18.6	3.8	28.9
	50-200	22.4	11.3	11.1	1.9	20.4	30.5	13.1	6.8
Other	0-50	1.8	22.3	0.6	5.4	0.2	3.7	1.1	14.0
	50-200	3.9	6.2	9.6	1.7	4.3	3.4	6.0	1.7

Table 3. Zooplankton composition in the 0-200 m layer of the western North Pacific Ocean (WP) and Bering Sea (WB) during day (d) and night (n). Sampling areas are indicated in Fig. 2.

| Zooplankton | Layer (m) | Composition (%) | | | | | | | |
| | | 5p (WP) | | 6p (WP) | | 8 (WB) | | 12 (WB) | |
		d	n	d	n	d	n	d	n
Copepoda	0-50	39.2	38.7	54.1	37.8	12.0	8.3	20.6	14.6
	50-200	33.9	38.0	40.2	22.4	16.5	13.5	26.1	12.5
Euphausiacea	0-50	1.8	8.5	0.8	21.9	0.8	35.8	0.1	21.5
	50-200	2.1	16.8	2.5	48.6	38.4	42.6	6.3	43.8
Amphipoda	0-50	2.7	6.9	2.5	4.3	2.7	1.9	3.3	3.8
	50-200	1.9	11.0	5.3	5.6	4.5	4.4	2.2	2.6
Pteropoda	0-50	0.1	0.1	0.4	0.1	0.0	0.0	0.0	0.0
	50-200	0.1	0.7	0.1	0.1	0.1	0.1	0.1	0.9
Sagitta	0-50	55.1	37.1	41.6	33.0	83.5	48.8	74.5	53.9
	50-200	52.0	24.3	43.7	22.3	28.0	29.6	58.0	36.5
Coelenterata	0-50	0.5	5.0	0.4	2.2	1.0	4.4	1.2	4.1
	50-200	8.5	5.9	4.4	0.6	10.3	8.8	5.0	2.9
Other	0-50	0.6	3.7	0.2	0.7	0.0	0.9	0.4	2.0
	50-200	1.5	3.2	3.8	0.5	2.1	1.0	2.3	0.7

account the daytime feeding habits of salmon, quantitative estimations of the plankton share of the diet should be calculated using the plankton community that lives in the 0–50 m layer in the daytime.

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Symposium Summary

Pacific salmon are the dominant group of fishes in the surface waters of the subarctic Pacific. Catches of Pacific salmon by all countries are also at historic levels. It is remarkable that one of the world's oldest and most important commercial fisheries is doing very well. The highest catches occurred in 1995, the second highest in 2005 (the year of the symposium) and the third highest catches were in 2003 (Fig. 1). Pacific salmon are also the indicator of the health of the ocean ecosystem that is most familiar to the general public. Ecosystem based management or the health of ecosystems has recently become a focus for most marine stewardship studies and many management agencies. Thus, it was natural that the North Pacific Marine Science Organization (PICES) with its focus on marine ecosystems and the North Pacific Anadromous Fish Commission (NPAFC) with its focus on Pacific salmon would combine efforts to assess the current status of Pacific salmon and explore the possibility that Pacific salmon provide measures of the health of large marine ecosystems.
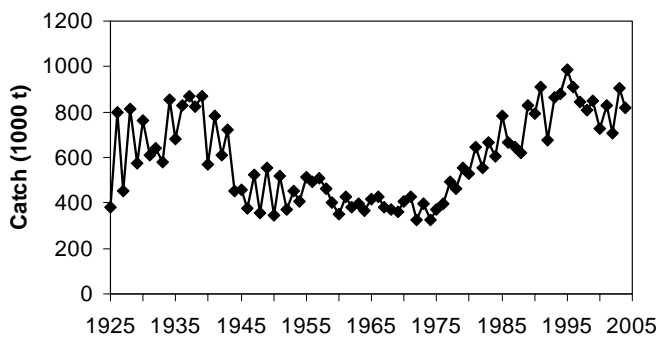

Fig. 1. The total catch of all species of Pacific salmon. The largest catch in history was in 1995 with the second largest in 2003. The catches in 2005 were after the symposium.

The proceedings took a little longer than usual to be published but Bulletin No. 4 contains the most recent information and interpretations of scientists studying the marine ecology of Pacific salmon. All papers were peer-reviewed with the objective to publish new information and new interpretations. A reader will see in the papers that there is very good cooperation among the scientists.

There are three main topics in these proceedings: (1) status of Pacific salmon, trends in abundance and biological characteristics; (2) role of Pacific salmon in the function of North Pacific marine ecosystems; (3) Pacific salmon as indicators of climate variability in the North Pacific and this bulletin is organized according to these topics. The symposium was held October 30 to November 1, 2005, in the Lotte Hotel on beautiful Jeju Island, Republic of Korea. Vladimir Radchenko and Dick Beamish co-chaired the symposium.

The organization of the symposium and the setting for the meeting allowed for good discussion despite the ever-present language barriers. Vladimir Fedorenko, the NPAFC Secretariat, and Toshinori Uoya in particular, worked hard to provide a flawless organization. There is no question that this was a successful symposium, as the papers in this bulletin will confirm.

The conference opened with the message that the best time to establish international cooperative research programs to improve forecasts of Pacific salmon is now, when abundances are at historic high levels. High seas research on Pacific salmon is expensive and it makes economic sense to integrate the research conducted by the member countries of PICES and NPAFC. Most scientists agree that the current high and low abundances of Pacific salmon are associated with favourable and unfavourable ocean and climate conditions. Whole life cycle studies that combine research efforts in fresh water and the ocean can be merged with the new technologies and the existing spirit of international cooperation to identify how climate regulates recruitment. A new cooperative research approach and open and direct communication with clients and patrons should increase research funding that will result in discoveries that will provide managers with the models needed to navigate the management of Pacific salmon through the uncharted waters of a changing climate.

Topic 1

There were 13 papers relating to the abundance and biology of Pacific salmon. It was evident that Pacific salmon in general are very healthy. Well-researched papers on the status of individual species were presented by Vladimir Radchenko, Alexander Kaev, Masa-aki Fukuwaka, Alexander Starovoytov, Doug Eggers, Bill Heard and Leon Shaul. There were examples of some stocks that were in low abundance off the coasts of British Columbia, Washington and Oregon, but the general trend was toward higher abundances. Several papers provided convincing evidence that the long-term trend of decreasing individual size had reversed and average sizes were typical of lengths at the beginning of the decline.

Diet studies are an essential contribution to the understanding of the linkage between ecosystems, ecosystem changes and Pacific salmon production. Detailed studies representing the results of extensive field research were presented by Vladimir Karpenko and Svetlana Naydenko. The importance of competition for food was assessed in a number of papers. Zavolokin and colleagues concluded that there was a low potential for feeding competition during their study in the western Bering Sea.

Papers from several Russian scientists provided perhaps

some of the best information available on the types of predators and their impact. It was suggested that an atlas of salmon injuries, symptoms of disease and prevalence of parasites be produced. This suggestion was enthusiastically supported by the audience; but the limitation is money. Included in this topic was the first report of the parasites of chum salmon in Korea.

Topic 2

There were 8 papers that described Pacific salmon distribution and the methods used to identify stocks and stock aggregates. Amazing progress has been made. Through cooperation and integration of research it has become possible to identify where stocks rear in the ocean seasonally throughout the entire period of their ocean residence. We are in the early stages of this research, but it is only a matter of money before we are able to use climate information and stock identification to model how climate is affecting marine survival in the open ocean as well as migration timing.

The research by Japanese scientists that has worked out the movements of chum salmon from juveniles to adults impressed the audience as chum salmon were shown to migrate south from the Bering Sea into the Gulf of Alaska in the winter and back to the Bering Sea in the summer. Elena Zavolokina summarized TINRO-Centre studies of chum salmon in the western Bering Sea. Go-Eun Kim and colleagues using SNPs proposed that chum salmon exist as three genetic population units. This was particularly interesting because of the large percentage of chum salmon that originate in hatcheries. New information on archival tags was reported by Trey Walker. These vertical migration graphs held the attention of the audience as participants theorized in their own minds why salmon undergo these sometimes extensive vertical migrations.

Kate Myers reviewed the distributions, migration routes, migration timing and feeding areas of Asian and North American Pacific salmon. She proposed that species, populations, age and maturity groups occupy different habitats in the open ocean and these niches can change in response to climate changes. Mitsuhiro Nagata reported that hatcheries in Japan would get the best production when fry were released into ocean waters ranging from 7 to 12°C. Eventually, such models may provide a method of forecasting the impacts of changes in coastal plankton composition, such as reported by Hiroki Asami and colleagues, and marine survival of Pacific salmon.

Topic 3

This was a challenging topic for participants. A major threat to the future management of Pacific salmon is climate variability. Natural variability has several modes, but it is the regime scale that appears most influential for Pacific salmon. A number of papers addressed the issue of the impact of climate variability but it was apparent that global warming impacts are not well understood. Masahide Kaeriyama looked specifically at the impacts of global warming on Pacific salmon of Asian origin. There was a better relationship between early marine survival and the coastal environment than the open ocean areas. Survival was related to growth in the coastal areas; and thus global warming impacts that affect the early rearing environment of chum salmon in the Sea of Okhotsk will have important impacts in Japanese chum salmon production. Dave Beauchamp showed how bioenergetic models can be used to identify the separate effects of temperature, food availability and food quality.

Ed Farley linked Pacific salmon early marine growth and recruitment through the critical size, critical period hypothesis. Results of studies of juvenile Bristol Bay sockeye, Prince William Sound pink salmon and coho salmon from British Columbia showed that sufficient growth in the first marine summer was necessary for subsequent marine survival. The size of Pacific salmon that return to the fisheries has intrigued researchers since Bill Ricker reported the trend in declining sizes. Jack Helle and Ole Mathisen assembled a team of international researchers to look at this issue with some surprising interpretations. Ole Mathisen died before this bulletin was published and I suspect that he would be as pleased to have his paper in these proceedings as we were to have him participate in the conference. The challenge of using Pacific salmon as indicators of ecosystem health was tackled head on by Peter Rand and Jim Irvine. Alexander Kaev looked at the factors affecting a pink salmon population at the southern limit of its distribution in the western Pacific. The study caught the attention of Canadian researchers because the major production of pink salmon in Canada occurs in the Fraser River which is also at the southern limit of its distribution. Day and night diet studies are rare; thus the results reported by Anatoly Volkov applied to the results of papers in all three topics.

In the time since the symposium, researchers continued to share data and interpretations. Scientists, managers of science and agencies funding research recognized the importance this international effort to share data and discuss cruise results annually. PICES and NPAFC need to find ways to complement each other's scientific strengths at a time that is exciting for researchers and potentially dangerous for salmon. A major result of the conference was an agreement to synthesize the existing knowledge about climate impacts on Pacific salmon in the ocean and to produce an international plan to focus on research and monitoring needs.

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